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# Energetics of high-speed running: integrating classical theory and contemporary observations

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<sup>1</sup>Locomotion Laboratory, Rice University, Houston, Texas; <sup>2</sup>Concord Field Station, Museum of Comparative Zoology, Harvard University, Bedford, Massachusetts; <sup>3</sup>United States Army Research Institute for Environmental Medicine, Biophysics and Biomedical Modeling Division, Natick, Massachusetts; <sup>4</sup>Flight Laboratory, Division of Biological Sciences, University of Montana, Missoula, Montana; and <sup>5</sup>Center for Human Performance, Texas Medical Center, Houston, Texas

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**Weyand, Peter G., and Matthew W. Bundle.** Energetics of high-speed running: integrating classical theory and contemporary observations. *Am J Physiol Regul Integr Comp Physiol* 288: R956–R965, 2005. First published December 2, 2004; doi:10.1152/ajpregu.00628.2004.—We hypothesized that the anaerobic power and aerobic power outputs during all-out runs of any common duration between 10 and 150 s would be proportional to the maximum anaerobic ( $\dot{E}_{an-max}$ ) and aerobic powers ( $\dot{E}_{aer-max}$ ) available to the individual runner. Seventeen runners who differed in  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$  (5 sprinters, 5 middle-distance runners, and 7 long distance runners) were tested during treadmill running on a 4.6° incline.  $\dot{E}_{an-max}$  was estimated from the fastest treadmill speed subjects could attain for eight steps.  $\dot{E}_{aer-max}$  was determined from a progressive, discontinuous, treadmill test to failure. Oxygen deficits and rates of uptake were measured to assess the respective anaerobic and aerobic power outputs during 11–16 all-out treadmill runs that elicited failure between 10 and 220 s. We found that, during all-out runs of any common duration, the relative anaerobic and aerobic powers utilized were largely the same for sprint, middle-distance, and long-distance subjects. The similar fractional utilization of the  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$  available during high-speed running 1) provides empirical values that modify and advance classic theory, 2) allows rates of anaerobic and aerobic energy release to be quantified from individual maxima and run durations, and 3) explains why the high-speed running performances of different event specialists can be accurately predicted ( $R^2 = 0.97$ ;  $n = 254$ ) from two direct measurements and the same exponential time constant.

anaerobic power; aerobic power; locomotion; metabolism; skeletal muscle

A. V. HILL (23, 24) provided the original physiological explanation for the characteristic relationship between performance and event duration. Using then record performances from competitive foot racing and swimming, he observed that, as the duration of an all-out effort increases from a few seconds to a few minutes, the speed that can be maintained decreases markedly; however, with increases from a few minutes to a few hours, speed decreases relatively little. Hill attributed the negative exponential relationship between performance and duration to the different sources of metabolic energy in the body that fuel short and long efforts.

Although many theoretical analyses in Hill's tradition have since come forth, his original conception of the temporal relationships between sources of metabolic energy and event

duration remains largely intact. The steep portion of the speed-duration curve that characterizes shorter efforts is attributed to rapid decrements in rates of anaerobic energy release with increments in event duration (31, 32), whereas the relatively flat portion of the curve that characterizes longer efforts is attributed to the relatively constant release of aerobic energy beyond an initial activation period. From a qualitative standpoint, post-Hill models (10, 17–19, 29, 35, 37, 38, 42–44, 51) have been in good agreement with available performance data.

Although Hill's general explanations continue to be widely accepted, experimental validation of the ideas he formulated three-quarters of a century ago remains substantially incomplete. Direct validation of the prevailing paradigms has been provided for the endurance but not the sprint portion of the speed-duration curves that he analyzed. The classical work of Costill, Daniels, and colleagues (13, 15, 16) established the relationship between measured indexes of maximal aerobic power ( $\dot{E}_{aer-max}$ ) and the endurance running performances of different individuals. These investigators found that different runners used essentially the same fraction of their  $\dot{E}_{aer-max}$  for all-out endurance efforts of the same duration. This observation provided a critical link between physiological measurements on individuals and endurance performance capabilities.

Although both old and new models of high-speed running performance propose similar ideas about the fractional availability of the maximum anaerobic power ( $\dot{E}_{an-max}$ ) and  $\dot{E}_{aer-max}$  (10, 17, 18, 26, 35, 42–44), these assumptions remain untested. This is partly because of the inability to accurately measure whole-body anaerobic energy release, an obstacle precluding the direct evaluation of the anaerobic components of these models. At present, Hill's original views and the more current models of high-speed running performance are essentially the same and widely accepted but experimentally untested.

We (8) have recently reported an empirical relationship that accurately predicts the high-speed running performances of individuals from two direct measurements and a single exponential time constant. We found that the speed-duration curves of seven runners, although appreciably different in absolute terms, were similar when expressed in relation to the maximum speeds supported by their respective  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$ . This observation allowed us to use the difference between these two speeds, or each runner's anaerobic speed reserve (5), to derive a single exponential time constant for predictive purposes. For

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these individuals, the approach was successful: the performances predicted for efforts spanning a 2-fold range of speeds and a 30-fold range of run durations agreed with the actual performances to within an average of 2.5% ( $R^2 = 0.94$ ).

Our new model appears to link direct measurements on individuals to their high-speed running performances with an accuracy similar to more established and fully validated endurance models (27). Although the predictive accuracy of our brief equation implies a common underlying relationship, the physiological basis of the apparent generality remains to be identified. Recognizing that predicted performances are influenced by both the anaerobic and aerobic maxima included in our equation, we postulated that the relative availability of the  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$  for an all-out run of any given duration would be the same for different individuals. Direct evaluation of this possibility would allow us to examine classical theoretical ideas that have gone untested as well as advance the physiological understanding of our new relationship.

In the interest of the most rigorous test of the idea of the similar fractional availability of  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$  during high-speed runs of common duration, we sought out trained subjects who would differ most in the cardiovascular and musculoskeletal physiology affecting high-speed running performance: sprint (S), middle-distance (MD), and long-distance (LD) runners. The muscle properties of competitive runners from different event specializations vary in accordance with the functional needs for speed and endurance (7, 14, 22, 36). The metabolic and mechanical properties of different muscle fiber types influence performance and fatigue during in vitro stimulations (9). Therefore, the physiological variation among these athletes provides the most likely test case in which our hypotheses would not apply.

We undertook this study to test two hypotheses. First, we hypothesized that estimated rates of anaerobic and measured rates of aerobic energy release, when expressed in relation to the individual maxima, would not differ for S, MD, and LD specialists during all-out trials of equal duration. Second, we hypothesized that the exponential time constants that would provide the most accurate predictions of high-speed running performance of S, MD, and LD specialists would not differ from one another.

## METHODS

### Experimental Design

Three primary design strategies were employed to test our idea that high-speed running performance conforms to a single general relationship. First, we recruited runners who were specialized to perform different discrete durations: S, MD, and LD runners. We anticipated this strategy would provide large differences in the  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$  available, rates of anaerobic (nonmitochondrial) and aerobic (mitochondrial) energy release during high-speed running, and absolute running speeds. Second, we opted to collect metabolic and empirical performance data on individual subjects, rather than using existing records or data sets and employing theoretical estimates of anaerobic power ( $\dot{E}_{an-max}$ ) and the time course of anaerobic energy release (1, 24, 29, 35, 37, 42–47). Third, we used inclined, rather than level, running to elevate the demands for metabolic power during the all-out running trials. We reasoned that the greater metabolic demands of inclined running would allow potential between-group differences in metabolic power and relative metabolic power outputs to be more easily detected.

The approach linking the availability of metabolic power to high-speed running performance was based on our recently reported relationship (8) and the logical framework below. Some elements of our logic were based on our experience with direct measurements (49), whereas others, particularly those related to anaerobic metabolism, were less certain given the present limitations of measurement. We knew a priori that the total metabolic rate supporting these high-speed runs would equal the sum of the rates of energy release from anaerobic and aerobic metabolism:

$$\dot{E}_{tot} = \dot{E}_{an} + \dot{E}_{aer} \quad (1)$$

where  $\dot{E}_{tot}$  represents the average total metabolic rate,  $\dot{E}_{an}$  is the average rate of anaerobic energy release, and  $\dot{E}_{aer}$  is the average rate of aerobic energy release during an all-out run of any duration. From previous work, we knew that rates of anaerobic energy release at cellular and tissue levels (6, 11, 32, 33) decrease exponentially with the duration of muscular activation and that whole-body rates, estimated indirectly, apparently decrease in a similar fashion (31, 39, 49). We hypothesized that decrements in  $\dot{E}_{an}$  with increments in run duration would be the same for different runners when expressed relative to  $\dot{E}_{an-max}$  available during running. Thus, for any runner, we expected the rate of anaerobic energy release for a run of a given duration to follow the equation

$$\dot{E}_{an}(t) = (\dot{E}_{an-max}) \cdot e^{(-k_1 \cdot t)} \quad (2)$$

where  $t$  represents the duration of the run,  $\dot{E}_{an}(t)$  is the average rate of anaerobic energy release during a run of duration  $t$ ,  $\dot{E}_{an-max}$  is the maximal rate at which anaerobic energy can be released during running,  $e$  is the base of the natural logarithm, and  $k_1$  is the coefficient of the exponent describing the decrement in  $\dot{E}_{an}$  with increments in run duration. From direct measurements of oxygen uptake during high-speed running (8, 31, 49), we knew that the average rate of aerobic metabolism during individual running trials would increase as an exponential function of run duration, up to the maximal rate of aerobic metabolism [here measured as an average over the entire trial duration, thus  $\dot{E}_{aer-max}(avg)$ ]. We hypothesized further that, for all-out trials of any given duration, the fraction of the  $\dot{E}_{aer-max}$  utilized would be the same for different runners; thus

$$\dot{E}_{aer}(t) = \dot{E}_{aer-max}(avg) \cdot [1 - e^{(-k_2 \cdot t)}] \quad (3)$$

where  $\dot{E}_{aer}(t)$  represents the average rate of aerobic energy release during a run of duration  $t$ ,  $\dot{E}_{aer-max}$  is the maximal rate of aerobic energy release (i.e., maximal  $O_2$  consumption), and  $k_2$  is the coefficient of the exponent that describes the increase in  $\dot{E}_{aer}$  as a function of the duration of the run. For runs throughout our 3- to 150-s duration range, we expected  $\dot{E}_{tot}$  to be less than  $\dot{E}_{an-max}$  and greater than  $\dot{E}_{aer-max}$ . In this respect, we conceptualized  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$  as the upper and lower boundaries for  $\dot{E}_{tot}$  during the high-speed runs of the durations in question. We postulated further that the decrements in  $\dot{E}_{tot}$  occurring with increments in run duration would be proportional to the difference between  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$ . Accordingly, we expected the metabolic rate of any runner for a high-speed run of 3–150 s to follow the equation

$$\dot{E}_{tot}(t) = \dot{E}_{aer-max} + (\dot{E}_{an-max} - \dot{E}_{aer-max}) \cdot e^{(-k_3 \cdot t)} \quad (4)$$

where  $\dot{E}_{tot}(t)$  represents the total metabolic rate for an all-out run of duration  $t$ , the other terms are as previously defined, and  $k_3$  is the coefficient of the exponent describing the decrement in the total metabolic rate from the anaerobic to the aerobic maximum ( $\dot{E}_{an-max} - \dot{E}_{aer-max}$ ) that occurs with increments in the duration of the all-out run. Given the preceding logic and our assumptions that rates of anaerobic and aerobic energy release during an all-out run of any given duration would be proportional to the maxima of the individual runner, we expected the value of  $k_3$  to be the same for all runners.

To estimate the  $\dot{E}_{an-max}$  available during running, we measured the top speed that an individual could maintain for eight steps (50) and



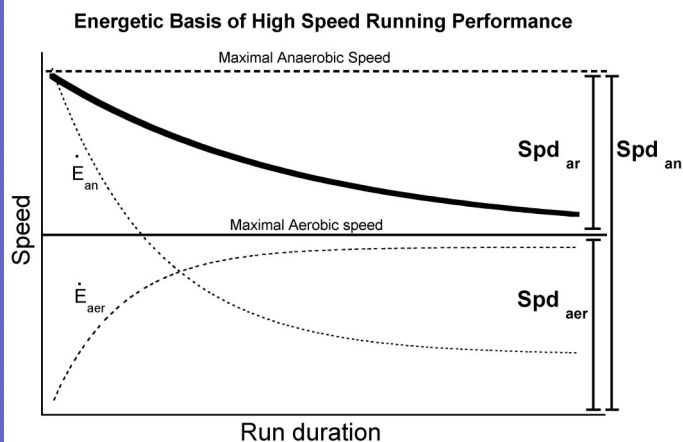


Fig. 1. Schematic representation of the proposed 3-parameter model of high-speed running performance. The horizontal lines represent the maximum speeds supported by anaerobic ( $\text{Spd}_{\text{an}}$ ) and aerobic power ( $\text{Spd}_{\text{aer}}$ ), respectively, whereas the difference between these two speeds ( $\text{Spd}_{\text{an}} - \text{Spd}_{\text{aer}}$ ) is the runner's anaerobic speed reserve ( $\text{Spd}_{\text{ar}}$ ). The lighter descending and ascending curves represent the trends in the metabolic power provided from anaerobic ( $\dot{E}_{\text{an}}$ ) and aerobic ( $\dot{E}_{\text{aer}}$ ) energy sources that support efforts of the durations illustrated. With increments in trial duration, decrements in the anaerobic power available exceed increments in aerobic power. Consequently, both the total metabolic power available and the all-out running speeds supported decreases as trial duration increases. All-out speeds for the durations in question can thus be described by 3 simple parameters: the maximum respective speeds supported by the anaerobic and aerobic power of the runner and an exponential constant that describes the shape of the speed-duration curve between the runner's upper and lower speed boundaries.

assumed here, as we did previously (8), that the metabolic rate-speed relationship is linear during inclined running (30). Although the validity of this assumption is not known, it enabled us to use running speed to test our second hypothesis directly. We simply substituted the running speeds supported by  $\dot{E}_{\text{an-max}}$  and  $\dot{E}_{\text{aer-max}}$  into Eq. 4 to obtain

$$\text{Spd}(t) = \text{Spd}_{\text{aer}} + (\text{Spd}_{\text{an}} - \text{Spd}_{\text{aer}}) \cdot e^{(-k_3 \cdot t)} \quad (5)$$

where  $\text{Spd}(t)$  is the speed of a run of duration  $t$ ,  $\text{Spd}_{\text{aer}}$  is the running speed supported by  $\dot{E}_{\text{aer-max}}$ ,  $\text{Spd}_{\text{an}}$  is the maximal running speed supported by  $\dot{E}_{\text{an}}$ ,  $e$  is as previously defined, and  $k_3$  is the coefficient of the exponent describing the decrement in running speed that occurs with increments of the duration of all-out running. In practice, we recognize that neither  $\text{Spd}_{\text{an}}$  nor  $\text{Spd}_{\text{aer}}$  relies exclusively on the respective energy sources. A schematic representation of our anaerobic speed reserve model appears in Fig. 1.

Our approach allowed us to test the validity of these ideas with four basic steps. First, we estimated the  $\dot{E}_{\text{an-max}}$  and measured the  $\dot{E}_{\text{aer-max}}$  available to each individual during running. Second, we assessed rates of anaerobic and aerobic energy release during 11–16 all-out treadmill runs lasting from 3 to 150 s. Third, we determined the relative availability of  $\dot{E}_{\text{an-max}}$  and  $\dot{E}_{\text{aer-max}}$  from the individual rates assessed during the trials. Fourth, we compared the  $k_3$  values for each of three subject groups that best predicted their all-out running speeds.

## Subjects

Seventeen trained collegiate and postcollegiate runners (5 S, 5 MD, and 7 LD) who were actively training at the time of the study volunteered and provided written, informed consent in accordance with the guidelines of the local institutional review board. Subjects met the following performance criteria: S specialized in racing distances of 400 m or shorter and had personal records in the 400-m dash of <50.0 s, MD specialized in either the 800 or 1,500 m and had personal records of <1:55 s in the 800-m run, and LD specialized in events 5,000 m or longer and could not run 400 m faster than 56.0 s. The physical, metabolic, and performance characteristics of the three groups appear in Table 1.

## Testing Protocol

All testing took place on a high-speed treadmill at an inclination of 4.6°. Subjects completed the entire testing protocol in four or five laboratory sessions, separated by a minimum of 2 rest days. The maximum speed supported by  $\dot{E}_{\text{an}}$  was determined in the last of these sessions, and the maximum speed supported by  $\dot{E}_{\text{aer}}$  was generally determined in the first. The maximum speed supported by  $\dot{E}_{\text{an}}$  was determined from a series of brief, progressive-speed runs (<10 s) up to the speed at which the subject was unable to complete eight steps without backward drift on the tread (50). The maximum speed supported by  $\dot{E}_{\text{aer}}$  was determined from a progressive, speed-incremented, discontinuous treadmill test to determine  $\dot{E}_{\text{aer-max}}$  and the metabolic cost of steady-state running similar to that reported previously (49). During the three intermediate sessions, five all-out trials at speeds expected to elicit failure between 10 and 220 s were administered in accordance with previous studies (8, 49). Subjects were instructed to take as much time as necessary for a full recovery between trials but were required to take a minimum of 10 min. Speeds for the all-out runs were selected so that each subject completed at least two runs within each of the following duration ranges: 12–30, 30–50, 50–80, 80–120, and >120 s. Each of the all-out runs was initiated by the subject lowering himself from the handrails onto the treadmill belt that was moving at a preselected speed. Complete weight transfer was typically accomplished within two to four steps and in <2 s. Subjects were instructed to terminate the run when they were physically unable to match the speed of the treadmill belt. At that point, they were instructed to grab the handrails and straddle the belt while it was stopped.

## Metabolic Measurements

**Maximal anaerobic power.**  $\dot{E}_{\text{an-max}}$  ( $\text{ml O}_2 \cdot \text{eq} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) was estimated from the maximal burst speed for eight steps (~3 s) achieved during all-out treadmill running. The corresponding metabolic power was estimated from a linear extrapolation of the relationship between speed and metabolic rate at lower running speeds to the maximum speed each runner achieved for a burst of eight steps. Initially, these runs were administered for durations of 10–15 s until we found measured rates of oxygen uptake that contributed as much as one-fourth of the estimated total metabolic energy required for these runs. Subsequently, for the last six subjects tested, we shortened these tests to eight steps without any backward drift on the treadmill

Table 1. Physical characteristics, metabolic power, and performance records

Group	n	Age, yr	Weight, kg	Criterion Event, m	Maximum Criterion Event Time, min:s	$\dot{E}_{\text{an-max}}$ , $\text{ml O}_2 \cdot \text{eq} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$	$\dot{E}_{\text{aer-max}}$ , $\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$
S	5	20.2 ± 0.4	74.9 ± 5.0	400	48.9 ± 0.7	138.0 ± 5.3	58.3 ± 2.4
MD	5	23.2 ± 6.2	73.3 ± 5.6	800	1:52.5 ± 1.6	131.9 ± 4.0	67.1 ± 1.9
LD	7	31.0 ± 4.6	69.7 ± 3.5	10,000	31:04 ± 1:25	113.4 ± 6.1	69.4 ± 1.6

Values are means ± SE. Age, mass, or height means did not differ ( $P < 0.05$ ) between sprint (S), middle-distance (MD), and long-distance (LD) runners.  $\dot{E}_{\text{an-max}}$ , maximum anaerobic power;  $\dot{E}_{\text{aer-max}}$ , maximum aerobic power.

belt in accordance with our previous description (50). Because the eight-step speeds provided a more valid indication of  $\dot{V}_{O_{2an}}$  and the earliest subjects were not available for retesting, the maximum eight-step speeds for the earliest subjects tested were extrapolated from the 15 data points on their individual speed-duration curve using Eq. 5 ( $t = 3$  s).

**Maximal aerobic power.**  $\dot{V}_{O_{2aer-max}}$  ( $\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) was determined during a progressive, discontinuous treadmill test consisting of 5-min bouts of constant-speed running interspersed with 3- to 6-min rest periods. The initial speed was 2.2 m/s. Speeds for subsequent bouts were increased by 0.15–0.3 m/s until a speed was reached at which the subject could not complete the 5-min bout while putting forth a maximal effort. Expired air was collected in Douglas bags during the fourth and fifth minutes of each bout. Aliquots from each bag were subsequently analyzed for oxygen (Beckman LB O<sub>2</sub> analyzer and Ametek S-3A oxygen analyzer) and carbon dioxide (Ametek CD-3A CO<sub>2</sub>) fractions after instrument calibration with gas of known O<sub>2</sub> and CO<sub>2</sub> concentrations. Minute volumes were determined with the use of a Parkinson-Cowan dry gas meter with simultaneous temperature determination using a digital TC thermometer (Wescor TH-65 TC thermometer). Rates of oxygen uptake (STPD) were determined in accordance with Consolazio et al. (12). Maximal rates were determined from the highest single minute value.  $\text{Spd}_{aer}$  was determined from the highest single minute value measured for  $\dot{V}_{O_{2aer}}$  and the linear regression of a minimum of six measured  $\dot{V}_{O_{2aer}}$  values below 90% of  $\dot{V}_{O_{2aer-max}}$  on running speed.

**Metabolic cost of running.** At speeds slower than the minimum eliciting the  $\dot{V}_{O_{2aer-max}}$ , the energy cost of running ( $\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) was determined from rates of oxygen uptake during the fourth and fifth minutes at each speed during the progressive discontinuous treadmill test. The metabolic rates required ( $\dot{E}_{tot}$ ) at speeds above the minimum speed eliciting  $\dot{V}_{O_{2aer-max}}$  were estimated by a linear extrapolation of each individual's oxygen uptake-speed relationship to the speed of the all-out run (29, 46). The potential limitations of these estimates have been discussed extensively (2, 3, 34). Despite the widespread use of the technique, the validity of the linear extrapolation is not known.

### High-Speed Running Measurements

**Rates of anaerobic energy release.** Average rates of anaerobic energy release ( $\dot{E}_{an}$ ,  $\text{ml O}_2 \text{ eq} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) for the all-out runs were calculated from the difference between the estimated total metabolic rate and the average rate of oxygen uptake during the run, i.e., the oxygen deficit (31, 49).

**Rates of aerobic energy release.** Average rates of oxygen uptake were determined for each of the all-out runs by collecting expired air in Douglas bags during the entire trial. Bag collection intervals were 30 s for the first minute and 60 s thereafter. The last bag of each trial was closed 1 s after the subject stopped running and grabbed the treadmill rails. Rates of aerobic energy release ( $\dot{V}_{O_{2aer}}$ ,  $\text{ml O}_2 \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ ) were determined as described for our measurements of  $\dot{V}_{O_{2aer-max}}$ .

### Data Analysis

Data analysis followed the hypotheses and equations of our model in the sequence of their appearance in the design section. Our first step was establishing values for speed,  $\dot{E}_{tot}$ ,  $\dot{E}_{an}$ , and  $\dot{V}_{O_{2aer}}$  for each subject at nine standardized run durations of 15, 20, 30, 45, 60, 75, 90, 120, and 150 s. Because the duration of all-out running could not be controlled to within a single second using treadmill speed, values at these nine standardized durations were interpolated in accordance with an iterative best-fit method (Kaleidagraph 3.51) and the aforementioned equations for the respective variables. Our second step was to use these individual values to determine group means for speed,  $\dot{E}_{tot}$ ,  $\dot{E}_{an}$ , and  $\dot{V}_{O_{2aer}}$  for S, MD, and LD at each of the nine standardized run durations.

Subsequently, to test our first hypothesis, we divided  $\dot{E}_{an}$  values by  $\dot{E}_{an-max}$  and  $\dot{V}_{O_{2aer}}$  values by  $\dot{V}_{O_{2aer-max}}$  at each of the nine durations to obtain the relative rates of anaerobic and aerobic metabolism,  $\dot{E}_{an}/\dot{E}_{an-max}$  and  $\dot{V}_{O_{2aer}}/\dot{V}_{O_{2aer-max}}$ , respectively.

Finally, to evaluate our hypotheses that the decrements in both  $\dot{E}_{tot}$  and speed with increments in run duration would be the same for different runners when expressed relative to the difference between  $\dot{E}_{an-max}$  and  $\dot{V}_{O_{2aer-max}}$ , we divided values of  $\dot{E}_{tot}$  above  $\dot{E}_{an-max}$  ( $\dot{E}_{tot} - \dot{E}_{an-max}$ ) by  $\dot{E}_{an-max} - \dot{V}_{O_{2aer-max}}$  of the runner [ $(\dot{E}_{tot} - \dot{E}_{an-max})/(\dot{E}_{an-max} - \dot{V}_{O_{2aer-max}})$ ]. Similarly, we divided the absolute speeds above the maximum speed supported by  $\dot{V}_{O_{2aer-max}}$  [ $\text{Spd}(t) - \text{Spd}_{aer}$ ] by the difference between the maximum speeds supported by  $\dot{V}_{O_{2an}}$  and  $\dot{V}_{O_{2aer}}$  ( $\text{Spd}_{an} - \text{Spd}_{aer}$ ) of the runner [ $(\text{Spd}(t) - \text{Spd}_{aer})/(\text{Spd}_{an} - \text{Spd}_{aer})$ ]. Our last step was to use the mean  $k_3$  value of derived empirically from a group of subjects who did not participate in this study ( $k_3 = 0.013 \pm 0.001 \text{ s}^{-1}$ ;  $n = 7$ ), run durations, and the measured maxima for the maximum speeds supported by the  $\dot{E}_{an}$  and  $\dot{V}_{O_{2aer}}$  of the runner to predict speed during each of the all-out runs completed (Eq. 5).

### Statistics

Group means of S, MD, and LD for absolute speeds and metabolic rates:  $\text{Spd}$ ,  $\dot{E}_{tot}$ ,  $\dot{E}_{an}$ , and  $\dot{V}_{O_{2aer}}$  at each of the nine standardized run durations were tested by a 3-by-9 ANOVA with a Scheffé's test of post hoc means. Similarly, group means for metabolic rates expressed in relation to individual maxima ( $\dot{E}_{an}/\dot{E}_{an-max}$ ,  $\dot{V}_{O_{2aer}}/\dot{V}_{O_{2aer-max}}$ ) and metabolic variables in relation to  $\dot{E}_{an-max}$  ( $\dot{E}_{tot} - \dot{E}_{an-max}$ ,  $\text{Spd}(t) - \text{Spd}_{aer}$ ,  $(\dot{E}_{tot} - \dot{E}_{an-max})/(\dot{E}_{an-max} - \dot{V}_{O_{2aer-max}})$ ,  $[\text{Spd}(t) - \text{Spd}_{aer}]/[\text{Spd}_{an} - \text{Spd}_{aer}]$ ) at each of the nine standardized durations were also tested by a 3-by-9 ANOVA with a Scheffé's test of post hoc means. Group means for empirically derived, best-fit values for  $k_1$ ,  $k_2$ , and  $k_3$  were tested by one-way ANOVA with a Scheffé's test of post hoc means. Simple linear regression was used to assess the proportion of variance in measured, all-out running speeds accounted for by the predictions of our model (Eq. 5). The a priori probability level considered significant for all statistical tests was  $P < 0.05$ . Original data, curve fits, and  $R^2$  values for speed,  $\dot{E}_{tot}$ ,  $\dot{E}_{an}$ , and  $\dot{V}_{O_{2aer}}$  for a representative subject appear in Fig. 2. Throughout the manuscript, means and standard error of the mean are reported.

## RESULTS

### Metabolic Maxima

**Anaerobic power.**  $\dot{E}_{an-max}$  values estimated from the eight-step burst running speeds conformed to expectations based on the event specializations of our subject groups, with mean values for S, MD, and LD being  $138.0 \pm 5.3$ ,  $131.9 \pm 4.0$ , and  $113.4 \pm 6.1 \text{ ml O}_2 \text{ eq} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ , respectively (Fig. 3). Means for S and MD were both statistically different from those of LD but were not different from each other. Because the energetic cost of running was similar among the three groups, the maximum eight-step burst running speeds that were attained closely paralleled the estimated  $\dot{E}_{an-max}$ . The  $\text{Spd}_{an}$  values for S, MD, and LD were  $8.6 \pm 0.1$ ,  $8.2 \pm 0.2$  and  $6.6 \pm 0.3 \text{ m/s}$ , respectively.

**Aerobic power.**  $\dot{V}_{O_{2aer-max}}$  values for all subjects tested were achieved with a mean respiratory exchange ratio of  $1.10 \pm 0.01$ . Means of the S, MD, and LD were  $58.3 \pm 2.4$ ,  $67.1 \pm 1.9$ , and  $69.4 \pm 1.6 \text{ ml O}_2 \text{ eq} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$ , respectively. Means for MD and LD were not significantly different, but both of these means were significantly greater than those of S. Because the energetic cost of running varied little among the three groups, the maximum speeds supported by  $\dot{V}_{O_{2aer}}$  were directly related to the respective values for  $\dot{E}_{an-max}$  (Fig. 3).

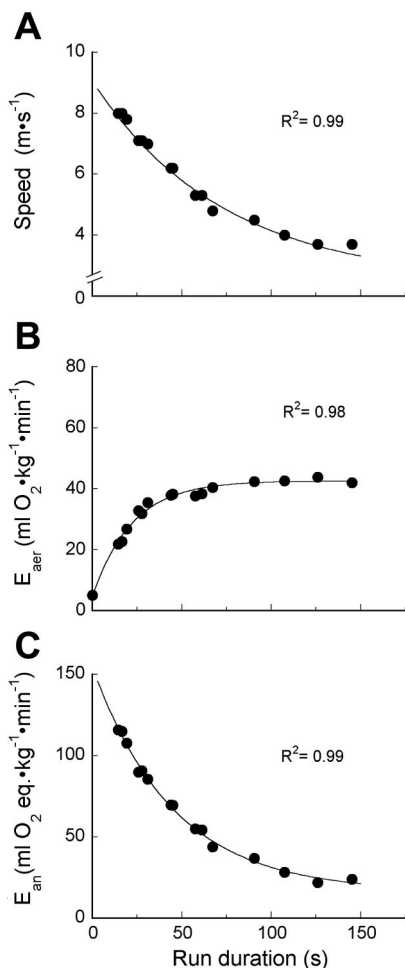


Fig. 2. All-out running speed (A) and average rates of  $\dot{E}_{aer}$  (B) and  $\dot{E}_{an}$  (C) as a function of run duration for a representative subject. Curves appearing for speed,  $\dot{E}_{aer}$ , and  $\dot{E}_{an}$  were fit with equations of the following forms:  $Spd(t) = Spd_{aer} + (Spd_{an} - Spd_{aer}) \cdot e^{(-k_1 \cdot t)}$ ;  $\dot{E}_{aer}(t) = \dot{E}_{aer-max}(avg) \times [1 - e^{(-k_2 \cdot t)}]$ ;  $\dot{E}_{an}(t) = (\dot{E}_{an-max}) \cdot e^{(-k_1 \cdot t)}$  (where max is maximum,  $t$  is duration of run, and  $k$  is a coefficient, as described in Eqs. 2–4).

The mean  $Spd_{aer}$  values for the S, MD, and LD were  $3.25 \pm 0.12$ ,  $3.96 \pm 0.16$ , and  $3.95 \pm 0.16$  m/s, respectively.

#### Speed and Metabolic Power as a Function of Run Duration

**Speed vs. run duration.** Group means for the decrements in speed with increments in the duration of all-out running from 3 to 150 s for S, MD, and LD were  $4.5 \pm 0.3$  (8.6 to 4.1),  $3.4 \pm 0.3$  (8.2 to 4.8), and  $2.25 \pm 0.2$  (6.6 to 4.4) m/s, respectively (Fig. 4).

**Absolute and relative rates of anaerobic energy release vs. run duration.** Average absolute rates of anaerobic energy release as estimated from oxygen deficits ( $\dot{E}_{an}$ ) differed significantly between each of the three groups for runs of many durations (Fig. 5A). None of the group means were significantly different for run durations of 120 and 150 s. The range of estimated rates of anaerobic energy release during all-out running spanned values of  $138 \text{ ml O}_2 \text{ eq} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$  for S during 3-s runs to values of  $20 \text{ ml O}_2 \text{ eq} \cdot \text{kg}^{-1} \cdot \text{min}^{-1}$  for LD during 150-s all-out runs. For each of the groups, the average rates of anaerobic energy release for the 150 s runs were

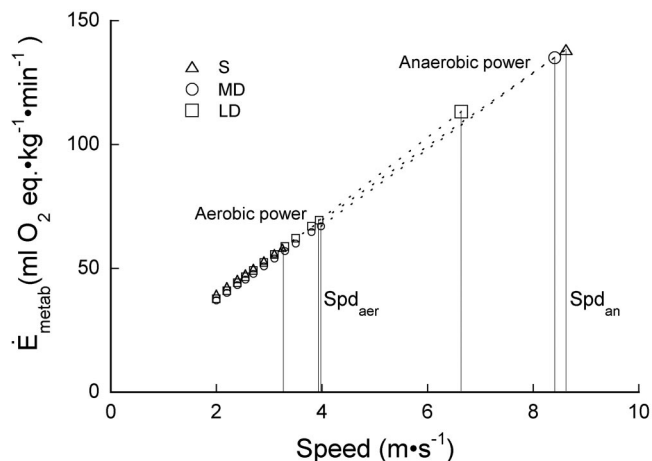


Fig. 3. Metabolic rates ( $\dot{E}_{metab}$ ), expressed in mass-specific units, as a function of running speed for sprint (S), middle-distance (MD), and long distance (LD) runners. These rates were measured directly at the speeds below the maximum speed supported by aerobic power (3 left vertical lines) and extrapolated to the maximum 3-s speeds (3 right vertical lines) for each group. Maximum rates of aerobic metabolism and the running speeds supported were greater for MD and LD compared with S, whereas maximum 3-s speeds and estimated maxima for anaerobic power were greatest for S, intermediate for MD, and least for LD.

one-fifth of those estimated for the 3-s runs (range of 0.18–0.20).

When absolute rates of anaerobic energy release were divided by the maximal rates estimated from an all-out 3-s run ( $\dot{E}_{an}/\dot{E}_{an-max}$ ), the absolute differences between the three groups were largely eliminated across all run durations (Fig. 5B). When expressed as fractions of the respective maxima, rates of anaerobic energy release for the three groups were not significantly different for 25 of the 27 total comparisons across the nine standardized durations. The means of the S were significantly greater than those of the MD for runs of 20 and 30 s.

The coefficient describing the exponential decrement in relative rates of anaerobic energy release with increments in run duration ( $k_1$  from Eq. 2) did not differ statistically between any of the three groups. Mean  $k_1$  values for S, MD, and LD were  $0.022 \pm 0.001$ ,  $0.025 \pm 0.002$ , and  $0.019 \pm 0.002 \text{ s}^{-1}$ ,

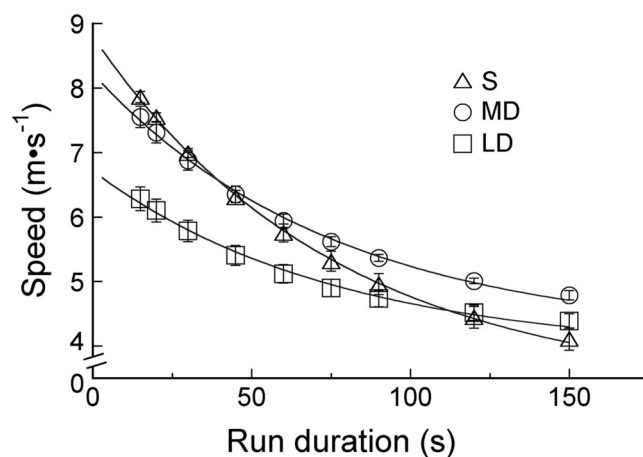


Fig. 4. Mean all-out running speeds as a function of run duration for S, MD, and LD at the 9 standardized run durations between 3 and 150 s. Decrements in speed with increments in the duration of all-out running were greatest for S, intermediate for MD, and least for LD.



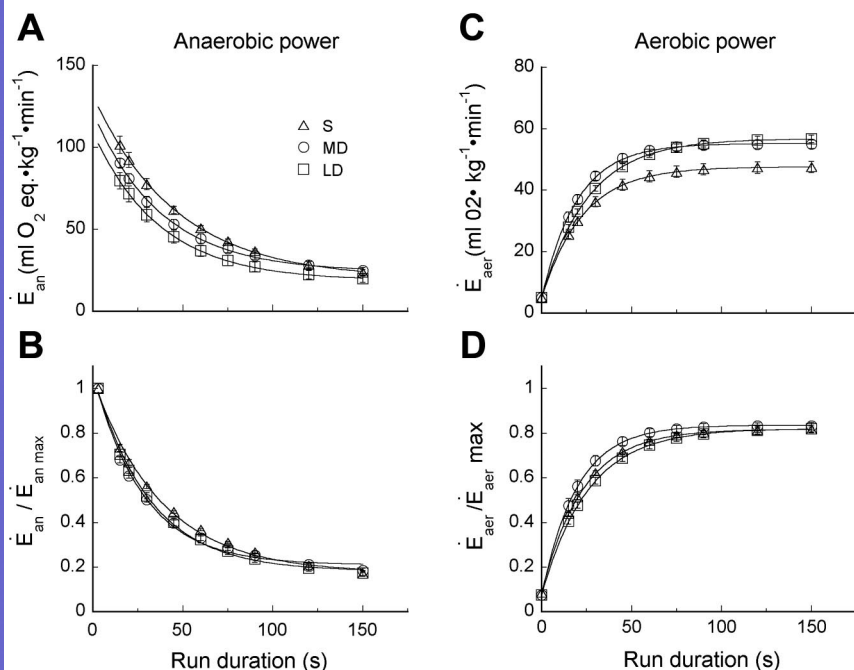


Fig. 5. Absolute and relative mass-specific rates of anaerobic ( $\dot{E}_{an}$  and  $\dot{E}_{an}/\dot{E}_{an-max}$ , A and B, respectively) and aerobic energy release ( $\dot{E}_{aer}$  and  $\dot{E}_{aer}/\dot{E}_{aer-max}$ , C and D, respectively), averaged over the course of all-out runs of 3- to 150-s durations for S, MD, and LD. Between-group differences in absolute rates of  $\dot{E}_{an}$  (A) and  $\dot{E}_{aer}$  (C) result from differences in  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$ , rather than different values for  $k_1$  and  $k_2$ . The between-group differences were largely eliminated when expressed relative to the group mean for maximum anaerobic and aerobic power, respectively.

respectively. For each of the groups, the run duration during which the rate of anaerobic energy release was one-half of the maximum was  $32 \pm 3$  s.

**Absolute and relative rates of aerobic energy release vs. run duration.** Average absolute rates of aerobic energy release ( $\dot{E}_{aer}$ ) were similar for MD and LD for all-out runs of all durations, whereas values for S were significantly lower than those of MD and LD at all of the standardized durations greater than 30 s (Fig. 5C).

When absolute rates of aerobic metabolism were divided by the  $\dot{E}_{aer-max}$  of the runner ( $\dot{E}_{aer}/\dot{E}_{aer-max}$ ), values for the S, MD and LD groups were not different in 25 of the 27 total comparisons over the nine standardized durations (Fig. 5D). The only means that differed significantly among the three groups at any of the nine durations were the greater values of the MD compared with LD for runs of 20 and 30 s.

The coefficient describing exponential increments in relative rates of aerobic metabolism with increments in run duration (i.e.,  $k_2$  from Eq. 3) did not differ between S and LD but was significantly greater for MD. Respective S, MD, and LD  $k_2$  values were  $0.045 \pm 0.002$ ,  $0.055 \pm 0.003$ , and  $0.039 \pm 0.002$  s<sup>-1</sup>. Rates of oxygen uptake increased sufficiently rapidly at the outset of all-out running such that the runners in each of the three groups were able to use 50% of their  $\dot{E}_{aer-max}(avg)$  for runs of  $15 \pm 1$  s.

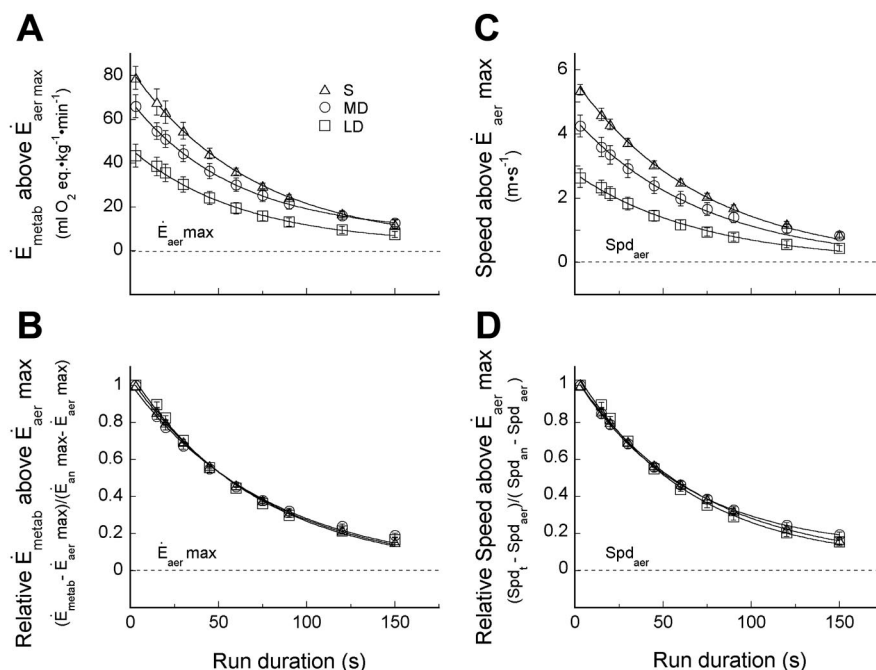
**Metabolic rates above  $\dot{E}_{aer-max}$  vs. run duration.** Estimated metabolic rates in excess of the aerobic maximum ( $\dot{E}_{tot} - \dot{E}_{aer-max}$ ) were significantly different for all three groups at most of the nine standardized run durations (Fig. 6A). However, when the rates in excess of the  $\dot{E}_{aer-max}$  for each of the three respective groups were divided by the difference between the maximal metabolic rate supported by anaerobic vs. aerobic power [ $(\dot{E}_{tot} - \dot{E}_{aer-max})/(\dot{E}_{an-max} - \dot{E}_{aer-max})$ ], there were no differences between group means at any of the nine standardized run durations (Fig. 6B). Thus, for S, MD, and LD alike, decrements in total metabolic rate with increments in run

duration were directly proportional to the difference between the maximal rates supported by  $\dot{E}_{an}$  and  $\dot{E}_{aer}$  ( $79.8 \pm 5.5$ ,  $64.7 \pm 5.4$ , and  $44.1 \pm 5.8$  ml O<sub>2</sub> eq·kg<sup>-1</sup>·min<sup>-1</sup>, respectively). The fraction of this difference that was maintained during all-out running fell from 100% for a 3-s run, to 75% for a 26-s run, to 50% for a 62-s run, and to 25% for a 126-s run.

**Running speeds above the maximum speed supported by aerobic power vs. run duration.** Absolute speeds in excess of the aerobic maximum [ $Spd(t) - Spd_{aer}$ ] were significantly different for all three groups at nearly all of the nine standardized run durations (Fig. 6C). However, when the absolute speeds in excess of those supported by  $\dot{E}_{aer-max}$  of each of the three respective groups were divided by the difference between the maximum speeds supported by anaerobic and aerobic power [ $(Spd(t) - Spd_{aer})/(Spd_{an} - Spd_{aer})$ ], there was no statistical difference between the group means at all nine of the standardized run durations (Fig. 6D). Thus, for S, MD, and LD alike, decrements in speed with increments in run duration were directly proportional to the difference between the maximum speeds supported by the anaerobic and aerobic power ( $5.4 \pm 0.2$ ,  $4.3 \pm 0.4$ , and  $2.7 \pm 0.3$  m/s, respectively). For all runners, the fraction of this speed difference ( $Spd_{an} - Spd_{aer}$ ) maintained during an all-out run fell from 100% for a 3-s run, to 75% for a 26-s run, to 50% for a 62-s run, and to 25% for a 126-s run.

The coefficient describing the decrements from the maximum speed supported by the  $\dot{E}_{an}$  to that supported by the  $\dot{E}_{aer}$  of the runner that occurred as the duration of all-out running became more prolonged did not differ statistically among the three groups. The statistical power for these comparisons ranged from 0.05 to 0.50. The mean  $k_3$  values for S, MD, and LD were  $0.0123 \pm 0.001$ ,  $0.0134 \pm 0.001$ , and  $0.0136 \pm 0.001$  s<sup>-1</sup>, respectively; the mean for all 17 subjects was  $0.0132 \pm 0.001$ .

Fig. 6. Metabolic rates and running speeds above the maxima supported by aerobic power [ $\dot{E}_{\text{metab}} - \dot{E}_{\text{aer}}$ , A, and  $\text{Spd}(t) - \text{Spd}_{\text{aer}}$ , C] for S, MD, and LD during all-out runs of 3–150 s. At all durations, metabolic rates and running speeds above the aerobic maxima were greatest for S, intermediate for MD, and least for LD. When the metabolic rates and speeds above the maximum supported by aerobic power were divided by the difference between the maximum metabolic rates ( $\dot{E}_{\text{an-max}} - \dot{E}_{\text{aer-max}}$ ) and running speeds ( $\text{Spd}_{\text{an}} - \text{Spd}_{\text{aer}}$ ) supported by anaerobic and aerobic power, between-group differences were all but completely eliminated (B and D, respectively).



The percentage of the difference between the maximum speed supported by  $\dot{E}_{\text{an}}$  and  $\dot{E}_{\text{aer}}$  (i.e., anaerobic speed reserve =  $\text{Spd}_{\text{an}} - \text{Spd}_{\text{aer}}$ ) that was maintained during all-out running was similar among the runners in each of the groups. For all subjects, the percentage of this speed difference ( $\text{Spd}_{\text{an}} - \text{Spd}_{\text{aer}}$ ) maintained fell from 100% for a 3-s run, to 75% for a 26-s run, to 50% for 62-s run, and to 25% for a 126-s run.

#### Actual vs. Predicted Speeds

The relation of the all-out running speeds measured vs. those predicted by our model appears in Fig. 7. The predictions illustrated were generated from Eq. 5 using run duration, the maximum respective speeds supported by  $\dot{E}_{\text{an}}$  and  $\dot{E}_{\text{aer}}$ , and an average  $k_3$  value from seven subjects who did not participate in

this study ( $0.013 \pm 0.001 \text{ s}^{-1}$ ). The overall average between the actual 254 all-out trial speeds of the subjects and the speeds predicted by Eq. 5 was 2.6% with a corresponding  $R^2$  values of 0.972.

Additional predictions were generated from the mean S, MD, and LD  $k_3$  values of 0.0123, 0.0134, and 0.0136  $\text{s}^{-1}$ . In each case, we used the mean  $k_3$  value, derived empirically for the subjects in each one of the three groups, to predict the all-out running speeds of the subjects in the other two groups. The predictions generated by the  $k_3$  values of the S, MD, and LD for the all-out trial speeds of the subjects in the other two groups agreed with the actual speeds to within an average of 2.5, 2.7, and 3.2% with corresponding  $R^2$  values of 0.967, 0.975, and 0.967.

To assess the possible influence of extrapolating burst speeds for some subjects, we performed two tests. First, we performed identical extrapolations on the six subjects for whom we had directly measured 3-s running speeds without including their measured 3-s values. In these six cases, the extrapolated speeds agreed with the measured values to within an average of  $0.24 \pm 0.08 \text{ m/s}$ . Second, for these latter subjects, we made separate predictions of the speeds of their all-out running trials using first their measured 3-s speeds and subsequently their extrapolated 3-s speeds. The  $R^2$  values from these separate predictions differed by  $<0.01$  and were slightly greater for the measured compared with the extrapolated values.

#### DISCUSSION

We obtained positive results to both of our hypothesis tests on the physiologically distinct subjects whose values were most likely to refute them. First, we found that the metabolic power outputs available during high-speed running, estimated for anaerobic metabolism and measured for aerobic metabolism, are direct functions of the maximum respective powers available to individual runners. Although the rates of anaerobic

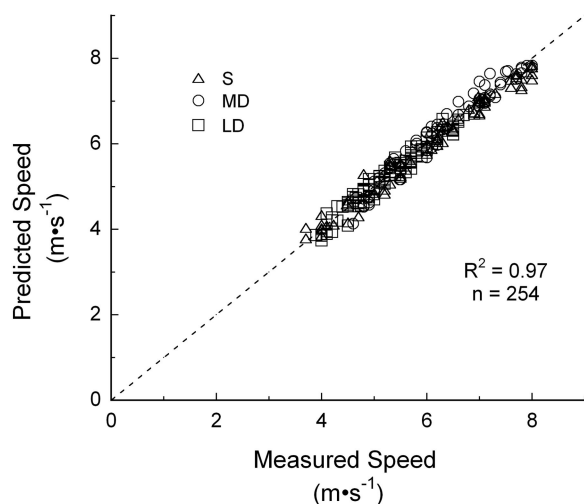


Fig. 7. Actual speeds vs. those predicted by Eq. 5 and a  $k_3$  value obtained from a separate group of subjects. The dashed line indicates the line of identity between predicted and measured performances.



and aerobic energy released by S, MD, and LD runners during all-out runs of common durations differed considerably in absolute terms, their values were largely the same when expressed in relation to individual maxima for  $\dot{E}_{an}$  and  $\dot{E}_{aer}$  (Eqs. 2 and 3, Fig. 5). Although this similar fractional availability has been an implicit and unstated assumption of theoretical analyses for more than 70 years, the data needed to evaluate these ideas were previously lacking. Our results demonstrate this phenomenon empirically and provide the exponential constants necessary to quantify the specific fractions available for all-out runs of known durations. Although many different values for these time constants appear in the literature (1, 18, 26, 35, 42, 45), the values presented here are the first to be based on direct measurements during high-speed running. In the absence of the similar fractional availability that we report here, the speed decrements that occurred between the speeds supported by each runner's anaerobic and aerobic maxima would probably not have been the same (Eq. 5, Fig. 6). Thus, in accordance with our second hypothesis, group values for  $k_3$  were not significantly different, and an independently obtained  $k_3$  value and individual values for  $Spd_{an}$  and  $Spd_{aer}$  accurately predicted the speeds of all of the trials completed by our subjects ( $R^2 = 0.97$ ,  $n = 254$ ). These results support the existence of a general relationship between the fractional availability of metabolic power and high-speed running performance.

#### A Common Basis for High-Speed Running Performance

The model we present for the metabolic basis of high-speed running performance has three components: the upper speed limit of the musculoskeletal system, which is set by the top speed of the runner; a lower limit for all-out speed, which is largely determined by the  $\dot{E}_{aer-max}$  of the runner; and the exponential decay factor, which describes the decrements in performance in relation to effort duration. We have postulated within the context of our model that our exponential constant quantifies a general relationship between the running speeds supported by the two primary sources of metabolic power in skeletal muscle, maximum performance, and effort duration.

The first component of our model, the  $\dot{E}_{an-max}$  available during running, was not quantified directly but was estimated from the all-out eight-step speeds of our runners. We were assured from previous reports that these burst speeds have a well-defined and measurable upper limit (41, 50). Although this strategy did not allow us to quantify the metabolic energy released during high-speed running directly, our results indicate that this mechanical limit has a direct influence on performance capabilities throughout the relatively broad range of durations investigated. Because we do not know the accuracy of our estimates of the metabolic power released from anaerobic sources in relation to run duration (2, 3, 34), we cannot know whether the empirical value that we derived ( $k_1$ ) for relating anaerobic energy release to the duration of all-out running is correct. The validity of this value cannot be determined in the absence of a valid method for determining the anaerobic energy released.

Regardless of the accuracy of the value for this constant, our results indicate that the mechanical function (i.e., speed) provided by anaerobic sources of metabolic power declines in a discrete and common manner from a measurable maximum

toward the respective maximum supported by  $\dot{E}_{aer}$  as the duration of running becomes more prolonged. Two mechanisms might explain a common relationship between metabolic power and function. First, an intrinsic link might result from the exponential decrements in cellular rates of anaerobic energy release as a function of the duration of muscular activation (6, 11, 28). Second, this decrement might result from the impairment in muscular force production and mechanical power output that coincides with a reliance on anaerobic metabolism in skeletal muscle (48). Regardless of the mechanism, performance capabilities for all-out runs of differing durations appear to be directly related to the relative reliance of the runner on anaerobic metabolism for speed.

We were able to quantify the second component of our model,  $\dot{E}_{aer-max}$ , in terms of both a supported speed and the amount of metabolic energy released per unit time. Our finding that the all-out speeds of different runners decreased from their maximum burst speed toward the  $Spd_{aer}$  in the same relative fashion as the duration of all-out running became more prolonged indicates that maximum  $\dot{E}_{aer-max}$  provides a baseline for performance during brief and intermediate duration all-out running (Eqs. 4 and 5). A direct implication of this result is that the close relationship between  $\dot{E}_{aer-max}$  and endurance widely recognized for long-distance running (13, 15, 16) applies to shorter events as well. This result explains why the speeds of highly aerobic runners, such as thoroughbred race horses and champion marathon runners, decrease little as the duration of high-speed running becomes more prolonged, whereas speeds of less aerobic short-distance specialists decrease markedly (24). Simply fueling a larger proportion of the active musculature with oxygen during all-out running allows runners to operate closer to the upper speed limit of the musculoskeletal system.

The third and temporal component of our model,  $k_3$ , describes the relative decrements in speed from the maximum supported by  $\dot{E}_{an}$  to that supported by  $\dot{E}_{aer}$  as run duration becomes more prolonged (Eqs. 1 and 4, Fig. 6D). Our results indicate that predictive accuracy can be provided by a single value. For example, the mean value that we derived from a separate group of subjects did not differ statistically from the one that we report here ( $k_3 = 0.013 \pm 0.001 \text{ s}^{-1}$ ;  $n = 7$ ; Student's  $t$ -test,  $\alpha \leq 0.05$ ,  $\beta = 0.94$ ). Thus, within the context of our model, we are confident that the same exponential value applies to athletes across the full spectrum of sprint to endurance specializations. Furthermore, our organismic level findings imply that a general relationship between sources of metabolic power and duration-dependent decrements in the mechanical function of skeletal muscle exists at both tissue and cellular levels and that this relationship is independent of the muscle fiber types and speeds that vary among S, MD, and LD runners (14, 22).

#### Integrating Classical Theory and Present Experimental Observations

Many dozens of models describing human running performance highs have been published over the past 100 years (for a historical review, see Ref. 4). For practical reasons, our discussion will be limited to the three most prominent models that relate high-speed running performance to the availability of metabolic power. The models of di Prampero and colleagues

(17, 18) assess all-out performances of durations ranging from 100 to 800 s. Their models include both theoretical and measured values and can achieve predictive accuracy similar to ours. Their primary objective was modeling performances lasting from 100 to 800 s, and, as these authors acknowledge, their models are most accurate for durations in excess of 200 s. In contrast, we have focused on the steep portion of the speed-duration curve because 70% of the duration-dependent decrements in performance that we report occur in the first 100 s.

Among the most frequently cited models are theoretical considerations of world record performances that do not incorporate direct metabolic measurements from the runners who achieved them (35, 42–44). These strictly theoretical models predict world record and world-leading performances to within 2% or less and the quantitative physiological descriptions that they present have been widely accepted (20, 21, 25). These models are formulaically similar to ours but are not supported by experimental data. Thus, as noted by Ingen Schenau et al. (26), the extent to which the predictive accuracy reflects the physiological reality is not known.

The results that we present here and present knowledge suggest that two quantitative refinements would improve the physiological accuracy of existing theoretical models. First, the values that these models provide for the fractional availability of  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$  can differ considerably from those that we assessed directly in our subjects here. The minimum trial duration during which our runners used an average of one-half of their  $\dot{E}_{aer-max(avg)}$  was 15 s rather than the 23 s, as theorized by Ward-Smith (43). Because our empirical values represent the average rates for each trial and do not include the oxygen taken up from the body's stores during the brief all-out trials, the 50% difference that we report is probably an underestimate. Although less certain, our estimates of the fractions of the  $\dot{E}_{an-max}$  available also exceeded the equivalent estimates made by Ward-Smith. The trial duration at which the fractional availability of the  $\dot{E}_{an-max}$  fell to 50% was 32 s vs. the 14 s estimated by Ward-Smith (46). His underestimates of the metabolic power contributed from both anaerobic and aerobic sources are likely offset by unrealistically high estimates of the mechanical efficiency (1).

A further physiological difficulty precludes applying these theoretical models to actual runners. The hypothetical runner created by Ward-Smith (42) is capable of world record or world-leading performances for an effort of any duration from 100 to 10,000 m. This athlete is required to have a  $\dot{E}_{aer-max}$  of 81 ml  $O_2 \cdot kg^{-1} \cdot min^{-1}$  (43) and a  $\dot{E}_{an-max}$  of 154 ml  $O_2 \cdot eq \cdot kg^{-1} \cdot min^{-1}$  (47). Although both of these values are likely possible for individual elite athletes, the physiological trade-offs involved in the optimization of speed vs. endurance would prevent any single athlete from possessing both of these powers. For example, the  $\dot{E}_{aer-max}$  of elite competitors vary over a considerable range and in accordance with the endurance requirements of the event (40). Similarly, the muscle properties that confer sprinting ability, rapid force development and relaxation, are achieved at the expense of endurance capabilities (36). The empirical values that we provide could be used to refine theoretical models and could also be applied to individual runners.

## Conclusions

Despite the dynamic, physiological conditions involved, we have demonstrated that high-speed running performance can be understood in terms of the  $\dot{E}_{an-max}$  and  $\dot{E}_{aer-max}$  of individual runners and the common time courses of their respective fractional availabilities. The dependence of skeletal muscle on the same basic metabolic pathways allows the empirical framework provided here to be useful for numerous purposes. Previously, we have used our exponential time constant,  $k_3$ , to develop a new technique for assessing performance and determining the  $\dot{E}_{an}$  and  $\dot{E}_{aer}$  maxima of individual performers (8). Additionally, our empirical framework could be used to analyze the relationship between metabolism and muscular performance in other modes of exercise or conceivably within individual muscle cells and tissues. Such investigations could determine whether skeletal muscle fatigue during whole-body exercise has the intrinsic, general, and quantifiable metabolic basis suggested by our findings.

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## REFERENCES

1. **Arsac LM and Locatelli E.** Modeling the energetics of 100-m running using speed curves of world champions. *J Appl Physiol* 92: 1781–1788, 2002.
2. **Bangsbo J.** Is the  $O_2$  deficit an accurate quantitative measure of the anaerobic energy production during intense exercise? *J Appl Physiol* 73: 1207–1209, 1992.
3. **Bangsbo J.** Quantification of anaerobic energy production during intense exercise. *Med Sci Sports Exerc* 30: 47–52, 1998.
4. **Billat V, Koralsztajn JP, and Morton RH.** Time in human endurance models: from empirical models to physiological models. *Sports Med* 27: 359–379, 1999.
5. **Blondel N, Berthoin S, Billat V, and Lensil G.** Relationship between run times to exhaustion at 90, 100, 120, and 140% of  $v\dot{V}O_{2max}$  and velocity expressed relatively to critical velocity and maximal velocity. *Int J Sports Med* 22: 27–33, 2001.
6. **Boobis LH.** Metabolic aspects of fatigue during sprinting. In: *Exercise Benefits, Limits and Adaptations*, edited by Macleod D, Maughan R, Nimmo M, Reilly T, and Williams C. London: Spon, 1987, p. 116–143.
7. **Booth FW and Thomason DB.** Molecular and cellular adaptation of muscle in response to exercise: perspectives of various models. *Physiol Rev* 71: 541–585, 1991.
8. **Bundle MW, Hoyt RW, and Weyand PG.** High speed running performance: a new approach to assessment and prediction. *J Appl Physiol* 95: 1955–1962, 2003.
9. **Burke RE and Levine DN.** Mammalian motor units: physiological-histochemical correlation in three types in cat gastrocnemius. *Science* 174: 709–712, 1971.
10. **Capelli C.** Physiological determinants of best performances in human locomotion. *Eur J Appl Physiol* 80: 298–307, 1999.
11. **Conley KE, Blei ML, Richards TL, Kushmerick MJ, and Jubrias SA.** Activation of glycolysis in human muscle in vivo. *Am J Physiol Cell Physiol* 273: C306–C315, 1997.



12. **Consolazio CF, Johnson RE, and Pecora LJ.** *Physiological Measurements of Metabolic Functions in Man.* New York: McGraw-Hill, 1963.
13. **Costill DL.** Physiology of marathon running. *JAMA* 221: 1024–1029, 1972.
14. **Costill DL, Daniels J, Evans W, Fink W, Krahenbuhl G, and Saltin B.** Skeletal muscle enzymes and fiber composition in male and female track athletes. *J Appl Physiol* 40: 149–155, 1976.
15. **Costill DL, Thomason H, and Roberts E.** Fractional utilization of the aerobic capacity during distance running. *Med Sci Sports Exerc* 5: 248–252, 1973.
16. **Daniels J and Daniels N.** Running economy of elite male and elite female runners. *Med Sci Sports Exerc* 24: 483–489, 1992.
17. **Di Prampero PE.** Factors limiting maximal performance in humans. *Eur J Appl Physiol* 90: 420–429, 2003.
18. **Di Prampero PE, Capelli C, Pagliaro P, Antonutto G, Girardis M, Zamparo P, and Soule RG.** Energetics of best performances in middle-distance running. *J Appl Physiol* 74: 2318–2324, 1993.
19. **Ettema JH.** Limits of human performance and energy-production. *Int Z Angew Physiol Einschl Arbeitsphysiol* 22: 45–54, 1966.
20. **Gastin PB.** Energy system interaction and relative contribution during maximal exercise. *Sports Med* 31: 725–741, 2001.
21. **Gladden LB.** Lactate metabolism during exercise. In: *Principles of Exercise Biochemistry* (3rd ed.), edited by Poortmans JR. New York: Karger, 2004, vol. 46, p. 152–196.
22. **Gollnick PD, Armstrong RB, Saubert CW, Piehl K, and Saltin B.** Enzyme activity and fiber composition in trained and untrained men. *J Appl Physiol* 33: 312–316, 1972.
23. **Hill AV.** The physiological basis of athletic records. In: *British Association for the Advancement of Science: Report of the 93rd Meeting*, 1925, p. 156–173.
24. **Hill AV.** The dimensions of animals and their muscular dynamics. *Sci Prog* 150: 209–230, 1950.
25. **Hochachka PW, Beatty CL, Burelle Y, Trump ME, McKenzie DC, and Matheson GO.** The lactate paradox in human high-altitude physiological performance. *News Physiol Sci* 17: 122–126, 2002.
26. **van Ingen Schenau GJ, Jacobs R, and de Koning JJ.** Can cycle power predict sprint running performance? *Eur J Appl Physiol* 63: 255–260, 1991.
27. **Joyner M.** Modeling: optimal marathon performance on the basis of physiological factors. *J Appl Physiol* 70: 683–687, 1991.
28. **Krustrup P, Gonzalez-Alonso J, Quistorff B, and Bangsbo J.** Muscle heat production and anaerobic energy turnover during repeated intense dynamic exercise in humans. *J Physiol* 536: 947–956, 2001.
29. **Lloyd BB.** The energetics of running: an analysis of world records. *Adv Sci* 22: 515–530, 1965.
30. **Margaria R.** *Biomechanics and Energetics of Muscular Exercise.* Oxford, UK: Clarendon, 1976.
31. **Medbø JI, Mohn AC, Tabata I, Bahr R, Vaage O, and Sejersted OM.** Anaerobic capacity determined by maximal accumulated O<sub>2</sub> deficit. *J Appl Physiol* 64: 50–60, 1988.
32. **Medbø JI and Tabata I.** Relative importance of aerobic and anaerobic energy release during short-lasting exhausting bicycle exercise. *J Appl Physiol* 67: 1881–1886, 1989.
33. **Medbø JI and Tabata I.** Anaerobic energy release in working muscle during 30 s to 3 min of exhausting bicycling. *J Appl Physiol* 75: 1654–1660, 1993.
34. **Olesen HL.** Accumulated oxygen deficit increases with the inclination of inclined running. *J Appl Physiol* 73: 1130–1134, 1992.
35. **Peronnet F and Thibault G.** Mathematical analysis of running performance and world running records. *J Appl Physiol* 67: 453–465, 1989.
36. **Rome LC and Lindstedt SL.** The quest for speed: muscles built for high-frequency contractions. *News Physiol Sci* 13: 261–268, 1998.
37. **Rumball WM and Coleman CE.** Analysis of running and the prediction of ultimate performance. *Nat Lond* 228: 184–185, 1970.
38. **Savaglio S and Carbone V.** Scaling in athletic world records. *Nat Lond* 16: 244, 2000.
39. **Scott CB, Roby FB, Lohman TG, and Bunt JC.** The maximally accumulated oxygen deficit as an indicator of anaerobic capacity. *Med Sci Sports Exerc* 23: 618–624, 1991.
40. **Spencer MR and Gastin PB.** Energy system contribution during 200- to 1500-m running in highly trained athletes. *Med Sci Sports Exerc* 33: 157–162, 2001.
41. **Volkov NI and Lapin VI.** Analysis of the velocity curve in sprint running. *Med Sci Sports Exerc* 11: 332–337, 1979, 1979.
42. **Ward-Smith JA.** A mathematical theory of running, based on the first law of thermodynamics, and its application to the performance of world-class athletes. *J Biomech* 18: 337–349, 1985.
43. **Ward-Smith JA.** The bioenergetics of optimal performances in middle-distance and long-distance track running. *J Biomech* 32: 461–465, 1999.
44. **Ward-Smith JA.** New insights into the effect of wind assistance on sprinting performance. *J Sports Sci* 17: 325–334, 1999.
45. **Ward-Smith JA.** Aerobic and anaerobic energy conversion during high-intensity running. *Med Sci Sports Exerc* 31: 1855–1860, 1999.
46. **Ward-Smith JA.** The kinetics of anaerobic metabolism following the initiation of high-intensity exercise. *Math Biosci* 159: 33–45, 1999.
47. **Ward-Smith JA and Radford PF.** Investigation of the kinetics of anaerobic metabolism by analysis of the performance of elite sprinters. *J Biomech* 33: 997–1004, 2000.
48. **Westerblad H, Allen DG, and Lannergren J.** Muscle fatigue: lactic acid or inorganic phosphate the major cause? *News Physiol Sci* 17: 17–21, 2002.
49. **Weyand PG, Lee CS, Martinez-Ruiz R, Bundle MW, Bellizzi MJ, and Wright S.** High-speed running performance is largely unaffected by hypoxic reductions in aerobic power. *J Appl Physiol* 86: 2059–2064, 1998.
50. **Weyand PG, Sternlight DB, Bellizzi MJ, and Wright S.** Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J Appl Physiol* 89: 1991–1999, 2000.
51. **Wilkie DR.** Equations describing power input by humans as a function of duration of exercise. In: *Exercise Bioenergetics and Gas Exchange*, edited by Cerretelli P and Whipp BJ. Amsterdam: Elsevier, 1980, p. 75–80.