

Running performance has a structural basis

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Summary

The body sizes of highly adapted human and other mammalian runners vary in accordance with specific performance needs. Sprint specialists are relatively massive and muscular while endurance specialists are conspicuously limited both in body and in muscle mass. We hypothesized that the greater body masses of faster specialists are directly related to the greater ground support forces required to attain faster running speeds. Using human runners as a test case, we obtained mean values for body mass, stature and racing speed for the world's fastest 45 male and female specialists, respectively, over the past 14 years (1990–2003) at each of eight standard track racing distances from 100 to 10,000 m. Mass-specific ground support force requirements were

estimated from racing speeds using generalized support force–speed relationships derived from 18 athletic subjects. We find a single relationship between mass, stature and event-specific ground support force requirements that spans the entire continuum of specializations and applies both to male and to female runners [body mass (kg)=mass-specific support force \times stature² (m) \times a constant; $N=16$ group means, $R^2=0.97$; where the ideal mass constant, $D=10 \text{ kg m}^{-2}$]. We conclude that running performance has a common structural basis.

Key words: locomotion, mechanics, ground support forces, muscle, tendon, bone, body mass index.

Introduction

The body sizes of highly adapted human and other mammalian runners vary in accordance with performance requirements. Sprinters have conspicuously greater body and muscle masses than slower endurance specialists. Although a relationship between locomotor specialization and morphology has long been observed among cursorial mammals (Gray, 1959; Hildebrand, 1960), the functional explanation for the structural basis of running speed is not known.

Classical evaluations of the relationship between structure and function in cursorial species considered the presumably enormous mechanical power requirements of fast running on level ground (Fenn, 1930; Hill, 1950; Gray, 1959). However, these early studies considerably overestimated the mechanical power that skeletal muscle must generate actively from metabolic sources during each stride. Cavagna's classical experiments later demonstrated that once a runner is up to speed, the large majority of the mechanical power needed to lift and accelerate the body and limbs during each stride is provided *via* conservative mechanisms of segment energy transfer and elastic recoil (Cavagna et al., 1964, 1971; van Ingen Schenau, 1998; Willems et al., 1995). These conservative transfer mechanisms greatly reduce the burden on skeletal muscle to serve as a *de novo* generator of mechanical power once a runner is up to speed (Kram and Taylor, 1990; Taylor, 1994). Thus, the possibility that faster specialists might

need additional body and muscle mass to meet mechanical power requirements does not seem likely.

In contrast to the relatively limited mechanical power muscle must generate during steady-speed running, musculoskeletal and ground support forces are considerable and depend directly on a runner's speed. During fast running, ground and muscle support forces can exceed the body's weight by as much as 2.5 and 5-fold, respectively (Weyand et al., 2000; Wright and Weyand, 2001). The large force requirements of high-speed running and the invariant force–area relation of skeletal muscle (Hill, 1950; Nelson et al., 2004) suggest that faster specialists may require relatively more muscle to generate these forces, and additional tendon and bone to transmit them safely (Biewener, 1989, 1993) to the ground. Accordingly, we hypothesized that the greater body masses of faster specialists are directly related to the greater ground support forces required to run at faster speeds.

Materials and methods

Experimental design

Several potential advantages led us to use human runners as an investigative tool. By contrast with other mammalian running species, accurate performance and body size data are available for hundreds of human runners with discrete

specialties spanning a broad range of distance and speed requirements. We assumed that the extensive data available for highly adapted, specialized human runners would provide representative body size optima for performance across the full continuum of specializations considered.

To maximize experimental rigor, we included specialized human runners of both sexes. We anticipated the presence of two sexes would increase the range of body masses and mass-specific support force requirements examined. Additionally, the inclusion of male and female runners who differ in body composition, but not in the force–area properties of their musculoskeletal tissues, should provide a more stringent test of the generality of the structure–function relationship proposed.

Our ultimate goal was to relate the body masses of specialized runners to their mass-specific ground support requirements. This required an appropriate standardization for the effect of height on body mass. In the simplest, and non-applicable case of identically proportioned individuals who differ in height (H^1), mass differences are proportional to height cubed (H^3). However, we knew *a priori* that the unique subjects in our sample would be similar in height but not identically proportioned (Khosla, 1978, 1985). On the basis of the well-established force–area properties of muscle, tendon and bone (Hill, 1950; Biewener, 1989, 1993; Nelson et al., 2004) we expected the mass variation of these unique subjects would occur largely in two dimensions (H^2) in accordance with their ground support force requirements. Therefore, we hypothesized that body masses related to height-standardized areas would vary in direct relation to mass-specific ground support force requirements. Thus, our hypothesis takes the following quantitative form:

$$M_b = F_g \times H^2 \times D, \quad (1)$$

where M_b is the ideal body mass for performance in kilograms, H is stature in meters, F_g is the ground support force in multiples of the body's weight, and D is an ideal mass coefficient in kg m^{-2} that quantifies the body mass per unit height-standardized area present to generate and transmit the required mass-specific force to the ground. The equation can be rearranged to express the ideal mass coefficient, D in terms of the ratio of body mass to height-squared (i.e. the body mass index, BMI) and requirement for mass-specific ground support force as:

$$M_b \times H^{-2} \times F_g^{-1} = D. \quad (2)$$

Since D is constant, Equation 2 indicates that for any given F_g required, a unique body mass index for optimal performance exists.

If the elite runners in our sample provide true body size optima for specialized human runners as we have assumed, our ideal mass coefficient, D , should have a slightly lower value for females than males. This result is expected because the density of the body's tissues varies between males and females. Given that the sex difference in body density is 2.5% for elite runners (Pipes, 1977) the value of D should be 2.5% lower for females than males.

Ground support force requirements

Generalized support force–speed relationships were formulated from direct measurements on nine athletic male and female subjects ($N=18$; 73.2 ± 6.6 and 60.8 ± 5.8 kg, respectively). All subjects provided written informed consent in accordance with the guidelines of the local institutional review board. Subjects ran at a series of constant speeds on a custom high-speed force treadmill. The average vertical force applied to the ground during the stance phase was determined in accordance with Weyand et al. (2000) during a series of constant speed runs from an initial speed of 2.5 m s^{-1} through the fastest speed each runner could attain for eight steps (range: males 2.5 – 11.2 m s^{-1} ; females 2.5 – 8.0 m s^{-1}). The slopes and intercepts of the linear best-fit relationships for each of the male and female subjects tested were averaged to obtain generalized support–force speed relationship for each sex. The horizontal and lateral forces applied were not included because their contribution to the total ground reaction force is quite small (Cavagna, 1975). The ground support force requirements of different specialists were estimated from their average racing speeds using the sex-specific force–speed equations formulated.

Body size optima

Mass and stature values for the world's fastest 45 male and female performers at each of eight standard track racing distances from 100 to 10,000 m ($N=275$ males and 261 females) during the past 14 years were compiled from public source data (*Track and Field News* 1990–2003). Individual athletes were included once in each event in which they were among the top 45 performers during this period. Height and weight values were coincident with each individual's best performance during this 14 year period.

Relative body masses and ground support force requirements

The hypothesis that a single structure–function relationship would apply regardless of sex and distance of specialization was tested by evaluating the proportion of variation (R^2) accounted for by the linear regression of body mass on the product of height squared and ground support force (Equation 1; $P < 0.05$). Also computed was the average difference between the mass predicted by Equation 1 and the actual mass for each of the 16 group means.

Results

Ground support force requirements

For both males and females stance-averaged support forces increased from values of 1.5 times the body's weight while running at slower speeds to as much as 2.5 times body weight during rapid sprinting. The support force–speed relationships derived for males and females were virtually identical (Fig. 1: males $y=1.27+0.105x$; females $y=1.24+0.106x$). The variability of individual intercepts (males ± 0.05 ; females ± 0.04) and slopes (males ± 0.006 ; females ± 0.01) from the respective sex

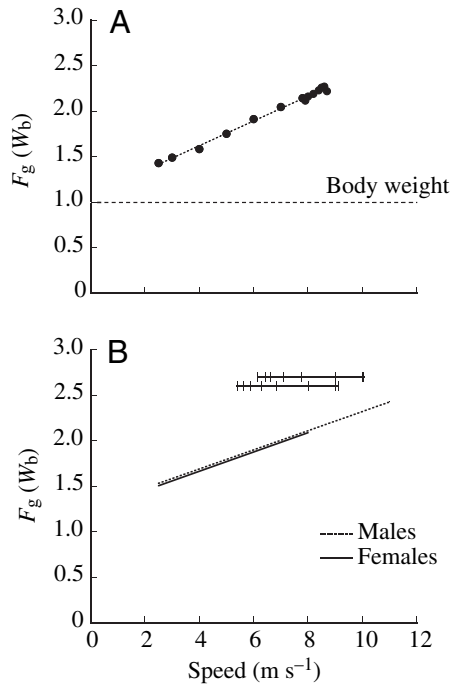


Fig. 1. Mass-specific stance-averaged support forces vs running speed. (A) stance-averaged force vs running speed in a representative subject; (B) mean stance-averaged support forces for athletic male (M; $N=9$) and female (F; $N=9$) subjects (M: $y=1.27 + 0.105x$; F: $y=1.24 + 0.106x$). Vertical hashes across the horizontal lines appearing in the upper portion represent the average race velocities of elite male and female specialists at each event distance. y -intercept values of F_g typically do not equal 1.0 because they are extrapolations beyond the range of speeds at which running is possible.

mean was also similar. Values reported throughout are mean \pm S.E.M.

Body size optima

Specialists in shorter distance races were generally more massive than those in longer ones. Within both sexes, the most massive specialists were those in the sprint events of 100, 200 and 400 m whose masses were roughly equal to one another. The body masses of athletes specializing in events of 800–10,000 m were inversely related to event distance for both sexes (Fig. 2A). Within each sex, the range of body masses among the eight different event specialists was 1.33- and 1.25-fold for males and females, respectively. The male mean from all eight events combined exceeded that of the females by 22.5% (66.4 ± 0.5 vs 54.2 ± 0.3 kg), with the single event sex differences ranging from 17.5 to 30.1% for the 3000 m and 100 m specialists, respectively.

Variation in stature was a third to a quarter of that for mass, and was related to event distance in a similar manner for males and females (Fig. 2B). Within respective sexes, height means spanned 1.09- and 1.06-fold ranges (males 400 m vs 10 km; females 400 m vs 10 km). For both sexes, the 400 m specialists were taller than those in any other event. The overall sex difference in stature was 6.0% (1.77 ± 0.003 vs 1.67 ± 0.004 m).

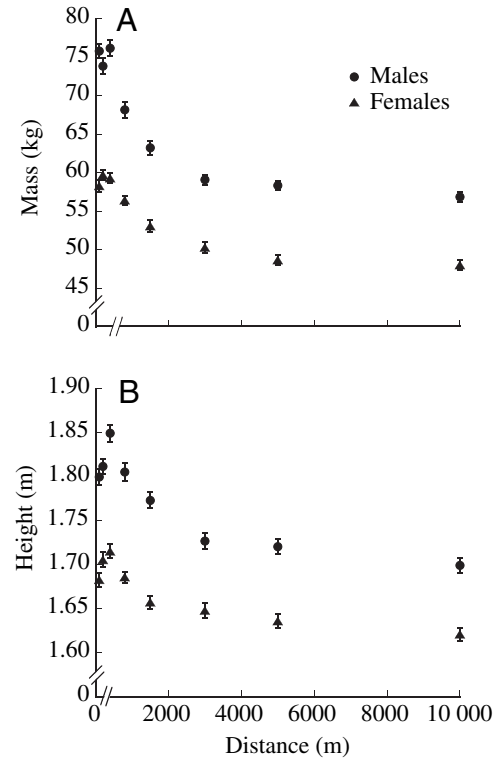


Fig. 2. Body sizes of elite specialists vs event distance (means \pm S.E.M.). (A) Body mass; (B) height.

By comparison with absolute mass, the relation of the body mass index to event distance was more consistent for males and females across the full range of event distances including the 100, 200 and 400 m (Fig. 3A). The mean BMI for all males exceeded that of all females by 8.5% (21.0 ± 0.1 vs 19.4 ± 0.08 kg m⁻²). Because stature has a direct influence on BMI values (among identically proportioned individuals) a 6.0% difference in BMI resulted from the males being 6.0% taller than the females. Thus, male values exceeded female values by 2.5% when the influence of height on BMI was removed.

Relative body mass and ground support force requirements

As a result of the direct dependence of ground support forces on speed (Fig. 1) and the slower racing speeds observed in longer races, the slope of the support force–event distance relationship was negative across the entire continuum of racing distances for males and females. The overall difference in support force requirements between males and females of 5.8% varied minimally across the eight different event distances (Fig. 3B, range 5.4–6.0%).

The mean ratio of the body mass index to mass-specific ground support force requirements (Equation 2) of different specialists was similar across the full range of event distances and not statistically different for males and females (Fig. 3C; males = 10.01 ± 0.04 , females = 9.81 ± 0.04 kg m⁻², $P=0.06$). In relation to the distance of specialization, the best-fit relationship between the BMI F_g^{-1} ratio and distance for all specialists

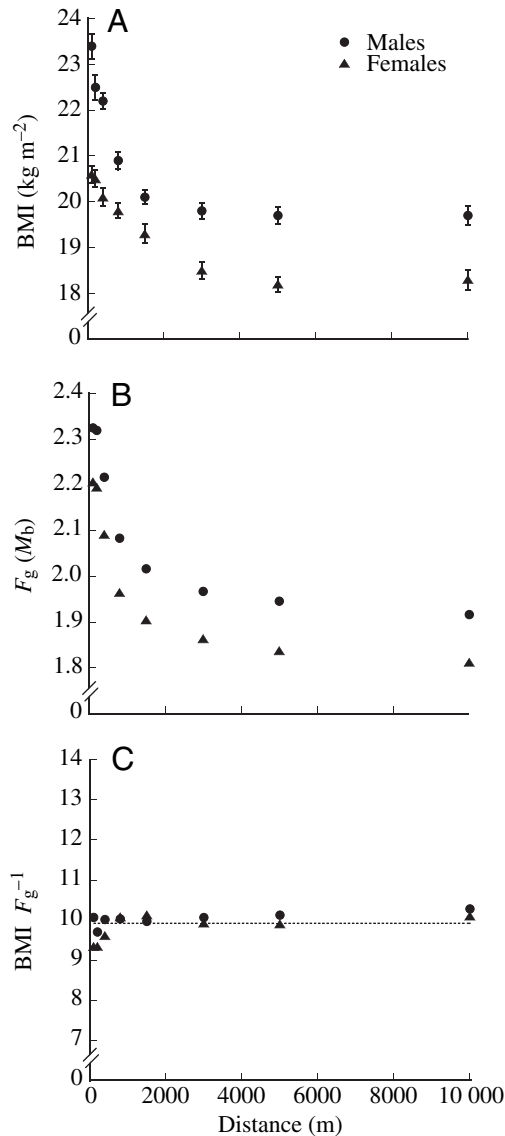


Fig. 3. Body mass index (BMI) and ground support forces vs event distance. (A) Body mass index; (B) ground support forces determined from the average racing speeds of event specialists; (C) the ratio of BMI to mass-specific ground support force of specialists vs event distance (mean BMI F_g^{-1} = 9.92 kg m⁻²; broken horizontal line).

increased by a factor of 1.04, from 100 to 10,000 m [kg m^{-2} (F_g^{-1}) = $9.8 + 0.00004 \text{ m}$, $R^2 = 0.27$; overall mean = 9.92 ± 0.03] with relatively greater deviation about the overall mean being present among the sprint specialists (range: 10.1–9.3).

Expressing the body mass means of the different event specialists in relation to the product of their event-specific support force requirements and height squared accounted for 97% of the total variability present among the 16 group means that spanned a 1.5-fold range of absolute values (Fig. 4; $M_b = -0.006 + 0.101x$; $R^2 = 0.97$; $P < 0.0001$).

The mean value of D of 9.92 ± 0.03 provided an average agreement of 1.32 kg between estimated and observed body masses for the 16 specialist means (range: 0.05–3.7 kg). Sex-

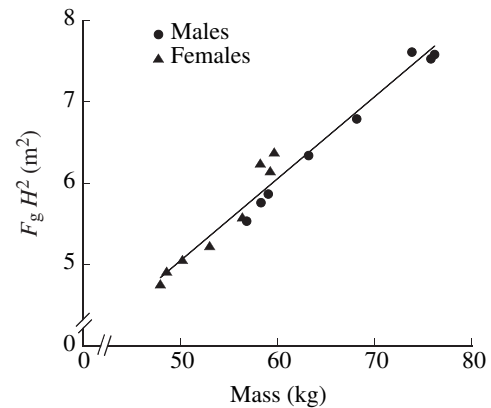


Fig. 4. The product of ground support force and height-squared in relation to body mass ($\text{mass} = -0.006 + 0.101x$, $R^2 = 0.97$).

specific values of D were 2.0% greater for males than females (males = 10.01, females = 9.81). These sex-specific values improved the accuracy of body mass estimates for each sex by 0.2 kg or less. The agreement between estimated and observed body masses was essentially unchanged when a rounded D value of 10.0 kg m⁻² was used for convenience (average agreement = 1.21 kg; range: 0.18–4.2 kg).

Discussion

Our idea that speed-specific ground support force requirements might explain the body mass variation present among highly adapted runners of different specializations was well supported by the elite human runners in our sample. Regardless of specialization or sex, we found that a single constant accurately links the ideal body mass for running performance to the ground support force required of the performer. Our original idea can be expressed as an ideal mass coefficient with a single convenient value: 10 kg of body mass per meter of height squared per unit body weight applied to the ground at the specialists racing speed. This coefficient provided mass estimates for the different specialists that were accurate to within an average of ± 1.2 kg, thereby accounting for 97% of the total mass variation present among the 16 group means (Equation 1, Fig. 4). The existence of a single structure–function relationship that links the mechanical requirements of running to the optimum body masses for performance has several basic implications. Most immediately, we can conclude that the fundamental determinant of body size optima for performance is the support force that runners apply to the ground at their racing speeds. Because different runners use the same biological tissues to satisfy this physical requirement, we find that running performance has a common structural basis.

How much mass does additional racing speed require?

The specific mass requirement we obtained for human running speed was relatively small. For male and female runners of the average heights of those in our sample (1.77

and 1.67 m, respectively) the respective masses required per one meter per second of racing speed were 2.5 and 1.8 kg. We attribute this modest mass requirement for speed to two factors. First, the specific support forces needed to increase speed are not large. Each meter per second requires an additional force of only one-tenth of the body's weight or less. Second, skeletal muscle generates force effectively. One kilogram of skeletal muscle can produce enough force to support 44 kg of mass (Hill, 1950; Nelson et al., 2004) given the average fiber lengths of the muscles in the human leg (Wright and Weyand, 2001). Given these force capabilities, we might have found mass minimums for human speed that were considerably smaller.

Biological necessity dictates that the ultimate mass requirement of human speed must be appreciably greater than any theoretical minimum estimated from tissue force–area properties. This is the case because our ideal mass coefficient includes all the tissues that contribute to the body's mass; not solely the musculoskeletal tissues involved in locomotion. Elite runners obviously cannot wholly eliminate the bodily tissues not directly involved in ground force application to become better adapted for performance. Given this minimum requirement for non-musculoskeletal tissue mass, effective skeletal muscle force production allows performance variation to be mediated by relatively small alterations in the body's musculature. Indeed, available evidence indicates that tissue adjustments necessary for modifying force production are present among runners of different performance specializations. The shorter distance specialists who are able to apply relatively greater mass-specific ground forces have proportionately more muscle in relation to body mass (Spent et al., 1993), and apply force with individual leg muscles, and muscle fibers that are a quarter to a third larger in area than those of endurance specialists (Lorentzon et al., 1988; Sjöström et al., 1988).

At the outset of the study we assumed that the non-musculoskeletal tissue masses of elite runners would be minimized to the extent genetically possible. In the case of fat tissue, sex-specific minima are well documented. For elite female vs male runners, the proportion of the body's mass comprising fat tissue is 7–8% greater, and the body's density is 2.5% less (Pipes, 1977). These body density differences led us to expect specific differences between males and females in the body mass to height-standardized area variables used here. In accordance with these expectations, we found the mean body mass indices of the elite male and female runners in our sample differed by 2.5%. Similarly, we found ideal mass coefficients that were 2.0% lower ($P=0.06$) for females than males. The agreement of both of our mass to area ratios with the established sex differences in body densities, as well as the similar differences before and after body masses were related to ground support force requirements, supports two of our initial assumptions. First, the body masses of the elite runners in our sample do represent the optima genetically possible for elite human male and female runners. Second, for male and female runners, the body masses that optimize performance are

similarly determined by the ground support forces their racing specializations require.

Why a single-function relationship?

The most basic explanation for why male and female runners of different specializations have the same mass requirement for providing ground support forces during running is that the muscles (Hill, 1950; Nelson et al., 2004) used to generate the necessary support forces, and the tendons and bones (Biewener, 1989, 1993) used to transmit these forces to the ground, have force–area properties that are essentially identical. The acute adaptation that these tissues undergo in response to habitual loading (Biewener, 1993) provides a mechanism for ongoing matching of tissue structure to the functional demands imposed by the training and racing regimens of individual specialists. However, the relationship between the support force applied to the ground and the functional loads ultimately imposed on the muscles, tendons and bones is also affected by the locomotor mechanics used by the individual runner. Any variability in stance limb posture; either among individuals or at different running speeds, would alter the muscle and tendon forces required per unit ground support force applied. Such variability would therefore be expected to have a direct effect on the mass requirement of running speed.

How variable is the mass requirement for running speed among individual performers? We cannot evaluate this question without direct measurements of ground support forces and the limb mechanics used by individual elite runners. The limited evidence available from non-competitive human runners indicates that stance limb mechanics vary only moderately between different runners (Biewener et al., 2004; Wright and Weyand, 2001) and vary little to not at all when the same individuals run at different speeds (Biewener et al., 2004). However, we did find appreciable variability in the two variables that determine the ideal mass coefficient most directly: the body mass indices of individual performers of any given sex and specialization, and the ground support forces required at common speeds for the 18 subjects on whom we formulated generalized relationships. Whether these factors co-vary so that the mass coefficients of each individual performer, like those of the 16 group means, conform closely to the value of $10 \text{ kg} \times \text{m}^{-2}$ obtained cannot be addressed at present. The virtually identical F_g –speed relationships obtained from independent samples of athletic male and female subjects supports the likely validity of our support force estimates for the population means of the large number of specialists included in each of the 16 groups. Thus, we are confident that we have correctly identified the biological value of the ideal mass coefficient even though we do not yet know how precisely this value applies to individual performers.

While ground support force requirements and the area-dependent properties of musculoskeletal tissues explain a minimum mass requirement, they do not explain the performance penalty imposed by having too much mass. We suggest that the ideal masses observed among specialists

represent a functional trade-off between the body and muscle mass minimums that maximize mass-specific aerobic power and endurance (Costill, 1972; Saltin, 1987; Daniels and Daniels, 1992) vs the additional musculoskeletal structure required to apply the greater ground forces necessary to race at faster speeds. This explanation is consistent with the observation that the capacity of the human cardiovascular system can be fully taxed when only a sub-fraction of the body's musculature is activated (Secher et al., 1974; Saltin, 1987). Additionally, the more limited mass-specific aerobic power maximums of shorter distance specialists are a direct result of their greater massiveness. When expressed absolutely, rather than in relation to their different body masses, the aerobic maxima of different specialists are nearly the same (Svedenhag and Sjodin, 1985; Daniels and Daniels, 1994; Weyand et al., 1994). In close keeping with the principle of economic design (Weibel et al., 1992), runners are optimized for performance when they meet their functional needs with the least amount of structure possible.

The functional trade-offs responsible for the body mass optima of the shortest distance specialists are less clear. Mass-specific aerobic power is relatively unimportant for sprinting (Weyand et al., 1999) and the positive relationship between mass, ground support force and speed implies that additional mass would allow sprinters to apply greater support forces and reach faster sprinting speeds. Sprinters clearly have not reached an upper adaptive limit to either muscle or body masses. Body builders and weight lifters of similar stature and body composition are considerably more massive than the elite sprinters in our sample (Spent et al., 1993; Johnson et al., 1990). At present, we can conclude that the structural optimum for human speed is set at an intermediate level of massiveness, but we cannot identify the factors imposing this moderate upper limit from the data presented here.

Concluding remarks

Previous analyses have noted that the area-dependent properties of the musculoskeletal tissues involved in locomotion can be challenging and even performance limiting for larger mammals and dinosaurs (Biewener 1989; Bennet and Taylor, 1995; Hutchinson and Garcia, 2002). Because area to mass ratios scale negatively with body size, larger animals are faced with the task of supporting relatively more mass with relatively smaller muscle, tendon and bone cross-sectional areas. To some extent, larger animals offset their intrinsic disadvantage for mass-specific force production by adopting a more favourable limb mechanical advantage for applying ground force. Their more erect stance limb postures reduce the muscle forces and cross-sectional areas needed to apply any given support force to the ground (Biewener, 1989). However, human runners do not appear to have this option. They suffer negative mechanical and metabolic consequences (McMahon et al., 1987; Farley and Gonzalez, 1996) when they deviate from the stance limb mechanics they choose naturally. In the absence of a functional option, human runners have simply adjusted structurally: musculoskeletal tissue areas are closely

matched to the support forces required. Thus, massiveness does not necessarily pose the performance disadvantages previously noted for large terrestrial vertebrates. Among runners of similar stature and body composition, being relatively more massive is not only beneficial for shorter distance specialists, but also appears to be biologically necessary for attaining faster speeds.

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