Scaling of Maximal Oxygen Uptake by Lower Leg Muscle Volume in Boys and Men

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Running head: \( \dot{V}O_2 \) max and muscle volume

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ABSTRACT

The aim of this study was to critically examine the influence of body size on maximal oxygen uptake (\(\dot{\text{VO}}_2\max\)) in boys and men using body mass (BM), estimated fat free mass (FFM), and estimated lower leg muscle volume (VOL) as the separate scaling variables. \(\dot{\text{VO}}_2\max\) and an \textit{in-vivo} measurement of VOL were assessed in 15 boys and 14 men. The FFM was estimated after percentage body fat had been predicted from population specific skinfold measurements. Using nonlinear allometric modeling, common body size exponents for BM, FFM, and VOL were calculated. The point estimates for the size exponent (95% CI) from the separate allometric models were: BM 0.79 (0.53 to 1.06), FFM 1.00 (0.78 to 1.22), and VOL 0.64 (0.40 to 0.88). For the boys, substantial residual size correlations were observed for \(\dot{\text{VO}}_2\max/BM^{0.79}\) and \(\dot{\text{VO}}_2\max/FFM^{1.00}\), indicating that these variables did not correctly partition out the influence of body size. In contrast, scaling by VOL\(^{0.64}\) led to no residual size correlation in boys or men. Scaling by BM is confounded by heterogeneity of body composition, and potentially substantial differences in the mass exponent between boys and men. The FFM is precluded as an index of involved musculature because VOL did not represent a constant proportion of FFM (VOL\(\times\)FFM\(^{1.45}\) (95% CI, 1.13 to 1.77) in the boys (unlike the men). We conclude that VOL, as an indicator of the involved muscle mass, is the most valid allometric denominator for the scaling of \(\dot{\text{VO}}_2\max\) in a sample of boys and men heterogeneous for body size and composition.

Key words: \(\dot{\text{VO}}_2\), allometry, MRI
INTRODUCTION

In nature, maximal oxygen uptake (\( \dot{V}O_2 \text{max} \)) is rarely attained and most individuals function routinely at submaximal metabolic rates. However, \( \dot{V}O_2 \text{max} \) is thought to be ecologically relevant and subject to selection (17). Furthermore, it sets the upper limit for relatively sustainable energy expenditure and, at least in adults, is inversely related to the risk of several chronic diseases (20).

A clear understanding of the development of \( \dot{V}O_2 \text{max} \) between childhood and adulthood is confounded by variability in body size and composition. The question of the influence of body size on energy metabolism has occupied researchers for 100 years (8). Accounting properly for the influence of body size on \( \dot{V}O_2 \text{max} \) requires detailed knowledge of size-function relationships. The most appropriate statistical model of size-structure and size-function relationships is provided by allometry (9). Huxley’s simple allometric equation, \( Y = aX^b \), has been employed most frequently in scaling studies (where \( Y \) is the structural or functional variable of interest, \( a \) is the proportionality coefficient, \( X \) is the body size variable [usually mass], and \( b \) is the size exponent). The resultant power function ratio – \( Y/X^b \) – is allegedly free from the confounding influence of body size.

To date, the most appropriate denominator for the power function ratio for scaling \( \dot{V}O_2 \text{max} \) has not been established, thus limiting our understanding of the size-function relationship in the growing child (26, 27). Using body mass (BM) as a general index of body size, reported size exponents for children and adults are variable, ranging from 0.28 to 1.10 (5, 11, 15, 26, 38). However, as approximately 90% of the oxygen passing through the lungs of a mammal
exercising at \( \dot{V}O_2 \) max is bound for a single sink in the skeletal muscle mitochondria (21), estimated fat free mass (FFM) may be a more judicious choice as an indicator of body size (9, 33, 35). Indeed, it was suggested half a century ago that any scaling analysis in humans should be based ideally on FFM, due to the often marked heterogeneity of body composition within human samples (13).

Although both BM and FFM have been used to scale \( \dot{V}O_2 \) max, at best they only provide a surrogate measure of the metabolically active muscle mass during exercise that elicits \( \dot{V}O_2 \) max. A direct quantification of the muscle, or at least a proportion of it, that is active during exercise should be used ideally to scale \( \dot{V}O_2 \) max. Magnetic resonance imaging (MRI) is a non-invasive technique that can be used to provide an \textit{in-vivo} quantification of muscle volume (34, 36), which could further our understanding of the influence of body size on \( \dot{V}O_2 \) max in the growing child. The number of studies that have attempted to quantify a proportion of the muscle volume that is active during dynamic exercise, and then examined its relationship with \( \dot{V}O_2 \) max in young people, is rather sparse (e.g., 12, 15, 36). Moreover, the results from these studies vary because of differences in the methods adopted to estimate muscle volume and the statistical methods that have been used to scale the \( \dot{V}O_2 \) max data by this body size variable. In light of the literature discussed above, the purpose of the current study was to investigate the most appropriate normalising factor (i.e., denominator) for \( \dot{V}O_2 \) max in children and adults of widely varying body size. To achieve this, non-linear allometric modeling procedures were used to critically examine the interplay between BM, FFM, muscle volume, and \( \dot{V}O_2 \) max.
MATERIALS AND METHODS

Participants

Fifteen boys (age 12.3(0.3) y) and 14 men (age 25.4(4.4) y) volunteered to participate in the study that was approved by the University Research Ethics Committee. The boys were recruited from a local secondary school, whilst the men were university students and staff personnel. All of the participants indicated that they were involved in a variety of recreational and competitive sporting activities. The boys’ parents and the men gave their written informed consent, whereas the boys assented to the procedures following an extensive familiarisation period. Completion of a pre-test health questionnaire indicated that all participants were asymptomatic and apparently healthy, with no stated contraindications to exercise.

Before any data were collected, the boys completed a structured familiarization session to become accustomed with treadmill running, reduce apprehension, and minimise metabolic measurement variability. Each boy completed between 20-30 minutes of walking and running on the treadmill at various speeds (4 to 10 km·h⁻¹) and gradients (0 to 8%). All participants (boys and men) were familiar with the procedures before data collection commenced. A self-assessment of secondary sexual characteristics by the boys was used to estimate physical maturity. The boys used drawings of the five stages of genitalia and pubic hair development to provide this information (23). The parents were asked to assist the boys with this assessment by, (i) discussing the schematic illustrations with them, and (ii) comparing their son's genital and pubic hair development with the schematics and accompanying written descriptions. Five and ten boys were at stages 2 and 3 for genital development respectively (median = 3), whereas six and
nine boys were at stages 2 and 3 for pubic hair development respectively (median = 3) (31). This would suggest that the boys were in the early to mid stages of puberty.

**Anthropometric Measurements**

Stature was measured to the nearest 0.01 m (Seca stadiometer 208), and BM to the 0.1 kg (Seca balance beam 710), with participants wearing only their running shorts and t-shirt. Skinfold thickness was measured to the nearest 0.2 mm using Harpenden callipers (John Bull, St. Albans, UK). All measurements were taken from the right hand side of the body, with the median of three measurements calculated as the fold thickness. Tricep and subscapular skinfold thickness were used to calculate the boys’ percent body fat (%BF) using maturation, race, and sex specific equations (29). The men’s %BF was calculated using the sum of four sites (tricep, bicep, subscapular and suprailiac) (14). The same experienced investigator took all of the skinfold measurements. The intra- and inter-investigator technical error of measurement in our laboratory using these sites with these populations are 3.8% and 5.7% respectively. Therefore, our measures meet the criteria for acceptability for skilled anthropometrists of < 5% and < 7.5%, respectively (25). Using BM and %BF it was possible to estimate FFM using the formula:

\[
FFM = \frac{100 - %BF}{100} \times BM
\]

**Treadmill Protocol**

In a temperature-controlled laboratory (19 to 22 ºC), each participant completed an incremental exercise protocol on a motorised treadmill (Woodway, Ergo ELG2, Germany) designed to elicit VO₂ max. Following an initial warm-up, participants ran at a fixed speed with the treadmill gradient being raised 1% each minute until volitional physical exhaustion (2). No holding of the
handrail was permitted during the test and strong verbal encouragement was given in the latter stages of the test. The starting speed was chosen to ensure exhaustion occurred between 8 and 12 minutes (10.0(1.5) min).

Measurement of \( \text{VO}_2 \max \)

Heart rate was monitored continuously via radio telemetry (Polar Accurex Plus, Kempele, Finland) as the participants ran on the treadmill. Expired air samples were collected into 150 L Douglas bags in each successive minute until the termination of the test. Oxygen and carbon dioxide concentrations in each Douglas bag were analysed using a paramagnetic oxygen analyser and an infrared carbon dioxide analyser (Servomex 1400, Sussex, UK), calibrated against gases of known concentration before each test. Volume of expired air was determined using a dry gas meter (Harvard, Kent, UK). For each sample, \( \text{VO}_2 \), expired carbon dioxide (\( \text{VCO}_2 \)), minute ventilation (\( \dot{V}_E \)), and respiratory exchange ratio (R) were calculated.

To verify an exhaustive effort, each participant had to satisfy at least two of the following criteria upon termination of the treadmill test due to volitional exhaustion: i) a plateau in \( \text{VO}_2 \) (\( \leq 2.1 \text{mL} \cdot \text{kg}^{-1} \cdot \text{min}^{-1} \)) with an increase in treadmill gradient, ii) a maximum heart rate \( \geq 95\% \) age predicted maximum (220 – age), and iii) \( R \geq 1.00 \) for the boys and \( \geq 1.10 \) for the adult men. In addition, all of the participants demonstrated overt signs of extreme physical exertion such as hyperpnea, sweating, facial flushing and grimacing, and unsteady gait at the end of the test. According to these criteria, all participants demonstrated a valid \( \text{VO}_2 \max \) (Table 1).

Measurement of Leg Muscle Volume (VOL)
Sequential axial plane MRI scans of the lower right leg using a fixed 0.2 T magnetic imaging scanner (E-scan, ESAOTE Biomedica, Genova, Italy) were used to measure VOL. Participants lay supine for the duration of the scans. Starting from the proximal head of the tibia (determined via ultrasonography), 3 to 4 contiguous 7 cm scans were performed distally towards the soleus-Achilles tendonous junction. A 7 cm scan above the proximal head of the tibia allowed the identification of the lateral and medial gastrocnemius insertions at the posterior of the knee joint.

A T1 weighted 3D isotropic profile with parameters set at; time to echo 16 ms, repetition time 38 ms, field of view 180 x 180 mm, matrix 256 x 192 pixels was used for each scan. The borders of each scan were marked using cod liver oil tablets, interpolated every 7 cm to prevent duplicate slice measurements. Each axial scan was divided into 7 x 1 cm slices. For every alternate 1 cm slice, the mean of three muscle anatomical cross-sectional areas (ACSA) measurements was calculated by tracing around the muscle using imaging software (NIH version 1.61/ppc, National Institute of Health, Bethesda, USA). By multiplying each of the ACSAs by the slice thickness (1 cm), with a further duplication to account for the missing slices during the analysis, VOL (mL) was estimated. Due to limitations of positioning the distal calf under the magnet, a 2nd order polynomial regression of the available data was used for each participant to extrapolate the remaining muscle volume to the soleus-Achilles junction (24). In order to calculate the error implicit to estimating the distal portion of the soleus in a sub-sample of the groups (n=10), direct measurement of the entire GM volume was compared with the GM volume obtained when the distal third of the muscle was estimated from the regression procedure described above. Using this method, the typical error of the predicted results compared with the direct measurement was 2.8% of the measured VOL. All scans were analysed by the same experienced investigator with an intra-observer variability of <3%.
Allometric Modeling Procedures

All statistical analyses were conducted using SPSS version 11.5 (Chicago, USA). Standard descriptives (mean(SD)) were used to characterize the groups of boys and men. Working in the arithmetic space defined by the original raw $X$ and $Y$ variables (1), we solved all model parameters by an iterative nonlinear protocol using the Levenberg-Marquardt algorithm, according to the following model:

$$\dot{V}O_2 \text{max} = a \cdot X^b \cdot \exp(c \cdot \text{group'})$$

(where $X$ is the body size variable of interest, and ‘group’ is a dummy variable coded ‘0’ for boys and ‘1’ for men). The above model derives a size exponent common to both groups. This process relies on the assumption that the slope of the relationship between the body size variable and the dependent variable does not differ substantially between groups. This assumption was tested by the addition of a ‘group by $X$’ interaction term to the above model. A non-significant interaction was revealed for all three body size variables, which implies homogeneity of regression slopes, that is, that a common size exponent can be applied appropriately to both boys and men. Age and physical maturation were entered initially into each allometric model as potential covariates, but neither made a substantial contribution to the regression model. All regression model assumptions (7) were satisfied. Power function ratios ($Y/X^b$) were constructed for each of the three scaling denominators from the equation derived from the above model by taking antilogs of the coefficient $a$ (for boys) and the constant plus the group coefficient ($a+c$) for men. The association between these power function ratios and the scaling denominators were then calculated using Pearson's product moment correlations. If the allometric model has been successful in partitioning out the influence of body size, then the correlation between the derived
power function ratio and the size variable should approach zero, that is, there should be little or no residual size correlation (32). Correlation coefficients that do not approach zero, regardless of whether they are statistically significant, would suggest that the power function ratio has not been completely successful in rendering \( \dot{V}O_2 \text{max} \) independent of body size.

**RESULTS AND DISCUSSION**

**Participant Characteristics**

The physical and physiological characteristics of the boys and men are shown in Table 1. The men were significantly taller, heavier, had greater FFM and VOL, but there was no difference in %BF when compared to the boys. When VOL was expressed per kg BM, the values were similar (24.1 boys vs. 26.0 men mL·kg\(^{-1}\)), but relative to FFM, the boys’ VOL was slightly lower (28.3 vs. 30.9 mL·kg\(^{-1}\)). Collectively, the participants were relatively heterogeneous for BM (31.4 to 97.9 kg), FFM (27.9 to 80.1 kg), and VOL (648 to 2416 mL).

**Allometric Modeling**

The regression output for the allometric models is summarised in Table 2. The common group exponents for each scaling denominator are shown, together with the exponents for boys and men separately. The separate group size exponents do not differ substantially between boys and men for the FFM and VOL variables, underlining the appropriateness of applying a common group exponent. For BM, the point estimate of the exponent for boys (0.96) appears larger than that for men (0.73). Although the Group x BM interaction term in the combined allometric model indicated that these exponents were not significantly different, this test is obviously influenced by sample size, and the difference may be real and important. Hence, the common
group exponent for body mass appears less robust than for the other two body size variables. In addition to the above issue, for reasons clearly articulated below we believe that BM is not an appropriate scaling denominator for normalizing $\dot{V}O_2$ max in boys and men.

The correlation coefficients between the power function ratios and the scaling denominators are shown in Table 3. For the men, the scaled variables were all clearly size-independent, with the point estimates for the correlation coefficient all negligible and approaching zero. However, for the boys the correlations for BM and FFM represent potentially substantial residual size correlation suggesting that these scaled variables may not be independent of body size. The smallest practically significant effect size for the correlation coefficient in this context is 0.1 (10). In the boys, the point estimate for the correlation between the power function ratio and the body size variable exceeded this threshold for both BM and FFM, suggesting meaningful residual size correlations. From the observed correlation coefficients in this sample of boys, the probability that the population correlation coefficient exceeds the smallest practically significant effect of $r = 0.1$ may be calculated, given the sampling variability (6). For FFM, the probability that the population correlation between the power function ratio and body mass exceeds 0.1 is 0.80. Hence, there is an 80% chance that the obtained residual size correlation of 0.33 is practically meaningful. For BM, there is a 54% chance that the observed residual size correlation of 0.13 is practically important. Based on this analysis, both BM and FFM, therefore, appear to be invalid allometric scaling denominators in the boys. In contrast, the residual size correlation for VOL in the boys was negligible and approaching zero, suggesting that the influence of body size had been partitioned out successfully by the $\dot{V}O_2$ max/VOL$^b$ power function ratio.
Collectively, these results suggest that only volume correctly partitions out the influence of body size for both boys and men.

Body mass may not adequately reflect the metabolically active skeletal muscle mass, due to heterogeneity of body composition across the sample. Moreover, the use of body mass as a gross surrogate of active muscle mass may be especially problematic in humans (compared with scaling studies in quadrupeds) as in bipeds running at \( \dot{V}O_2 \) max does not involve whole-body musculature (19). Theoretically, the confounding factor of variability in body composition within the sample may potentially be addressed, in part, by scaling by estimated FFM. However, scaling by FFM relies on the assumption that the involved, metabolically active muscle mass at \( \dot{V}O_2 \) max represents a constant proportion of FFM across the sample. We tested this assumption for the current study. In men, leg muscle volume is proportional to FFM\(^{0.98}\) (95% CI, 0.57 to 1.40), indicating that leg volume comprises a relatively constant fraction of FFM across the size range. In boys, however, leg muscle volume is proportional to FFM\(^{1.45}\) (95% CI, 1.13 to 1.77), revealing that the proportion of FFM comprised of leg muscle volume is not constant, and increases as a function of increasing body size (Figure 1). This disproportionate relationship between leg muscle volume and estimated whole body FFM reflects the change in the proportion of lower extremity muscle mass relative to total muscle mass. At birth it represents \(~40\%\) increasing to \(~55\%\) at full biological maturity (23). Furthermore, as boys enter puberty there is a dramatic increase in muscle mass relative to other lean tissues. The self-assessment of secondary sexual characteristics suggests that the boys in our study were in the early to mid stages of puberty, which would account for the relationship between VOL and FFM (Figure 1). This
reinforces the fact that FFM cannot be used legitimately as the scaling denominator to normalize the \( \dot{V}O_2 \) max of boys and men in this study.

The body mass relative and absolute \( \dot{V}O_2 \) max scores for the boys and adults are similar to those reported previously using treadmill ergometry (4, 28). We used MRI to measure leg muscle volume \textit{in-vivo}; unlike anthropometric techniques, these data are not confounded by subcutaneous fat or bone tissue. It was not possible to measure the volume of a larger proportion of the active musculature in our study due to the size of the scanner. However, other studies using MRI proton relaxation times, muscle glycogen depletion, and EMG recordings provide convincing evidence that the lower leg musculature is involved substantially during walking and running exercise, with a muscle activation higher (particularly for the plantar flexors and dorsi flexors, 18) or comparable to the thigh muscles including quadriceps, hamstrings, adductors, and gluteals (e.g., 30). Although we acknowledge that the lower leg volume represents a relatively small proportion of the total muscle volume involved during running exercise that elicits \( \dot{V}O_2 \) max, the plantar flexors and dorsi flexors play a key-role in locomotion, propelling the body forward during the push-phase and for clearing the foot off the surface during the swing phase. In fact, during the step-cycle the EMG activities of the tibialis anterior and of the gastrocnemii and soleus are two to three-fold longer those of the vastus lateralis and biceps femoris (18).

Besides, in the current study we are concerned primarily with the nature of the allometric relationship between muscle volume and \( \dot{V}O_2 \) max. Making the reasonable assumption of a proportional relationship between leg volume and the total volume of involved musculature in boys and men, indicates that the value of the scaling exponent ‘b’ in the allometric relationship would be unaffected by the absolute muscle volume included in the model. Hence, for the
purpose of deriving a valid allometric relationship to correctly partition out the influence of body size on $\dot{V}O_2$ max, we believe that the leg muscle volume is adequately representative of the involved musculature during running in bipeds.

Armstrong and colleagues (3, 5) used multilevel regression modelling in a large group of boys and girls to determine what factors might explain longitudinal changes in absolute peak $\dot{V}O_2$ during growth and maturation. A sample specific BM exponent of 0.88 (SE 0.04), which is similar to the common exponent in our study (Table 2), was given when an estimate of body composition was included in the model along with biological maturity, sex, and chronological age. The authors concluded that the change in FFM was the most important factor when considering the progressive divergence in peak $\dot{V}O_2$ between the boys and girls as they aged from 11 to 17 years. More specifically, they speculated that greater relative changes in muscle mass would facilitate the use of oxygen and enhance venous return via the peripheral muscle pump, thus augmenting stroke volume in the boys (3). When a measurement of active muscle mass is available, our data do not support the notion that FFM per se is the most important factor to consider when scaling $\dot{V}O_2$ max. However, in the absence of a muscle size measurement, this supposition is understandable.

To our knowledge, this is the first study to appropriately examine the scaling of $\dot{V}O_2$ max in a heterogeneous sample of boys and men using measurements of muscle volume in-vivo. However, some other studies have examined the relationship between $\dot{V}O_2$ max and body size in young people, albeit using different body size measures or when comparing males and females (5, 11, 12, 15, 36, 37). Using MRI to measure thigh muscle volume in 16 prepubertal boys, Welsman et
al. (36) reported that this body size parameter was related to absolute peak \( \dot{V}O_2 \) \((r = 0.80, P < 0.01)\). Furthermore, an ANCOVA analysis revealed an exponent of \( b = 0.55 \) (SE 0.08) when using thigh muscle volume as the scaling variable. Although this point estimate is within the 95% CI that we found when scaling \( \dot{V}O_2 \) max using leg muscle volume (Table 2 – combined model), interstudy differences in the samples and muscle volume measurements preclude a direct comparison. In two separate studies involving late adolescent girls (15 to 17 years old) and pre-to early-pubertal girls (8 to 10 years old) respectively, Eliakim et al. (15, 16) explored the relationships between exercise training, thigh VOL, maturation, and peak \( \dot{V}O_2 \). Results from both longitudinal and cross-sectional analyses were reported (15, 16). When the data for all 84 girls were pooled together, the BM exponent for peak \( \dot{V}O_2 \) was only 0.28 (SE 0.07). This value is extremely low in comparison with the 0.79 (SE 0.30) in the current study, but also relative to all other studies with this population. An exponent of only 0.28 suggests that as body mass increases within the sample of girls, the concomitant change in peak \( \dot{V}O_2 \) is proportionally much smaller. Although the difference between changes in BM and peak \( \dot{V}O_2 \) fits with most other allometric analyses of this relationship (i.e. \( b < 1 \)), the rate of change is far lower than expected. It would appear that the difference in thigh VOL from 9 to 16 years of age was smaller than expected (~8%) and it was suggested that this is the most likely cause for the unusual finding (15). Group differences between the two maturity groups were not found when aerobic capacity was expressed per thigh VOL using the ratio standard (mL·mL\(^{-1}\)·min\(^{-1}\), 15). However, our results suggest that this comparison may not control appropriately for differences in VOL. The scaling exponent for thigh muscle volume in Eliakim's study (15) was very similar to the VOL value for the boys in our study (0.69 vs. 0.64 respectively), albeit from different muscles. This finding lends additional support to our contention that the leg volume is adequately representative of the
involved musculature in exercise at \( \dot{V}O_2 \) max. Unfortunately, a comparison of the power function ratios for peak \( \dot{V}O_2 \) using the exponent was not made between the 9 and 16 year old girls, thus precluding an indirect comparison with our results.

We do not purport that our data are adequate for determining a precise or optimum value of the size exponent that may be generalized to the population – an endeavour that has been termed the ‘search for the Holy Grail’ (27). The observed point estimates for the exponents represent the ‘best guess’ of what the population exponent may be. The 95% confidence intervals surrounding these estimates are interpreted commonly as the likely range within which the population exponent will lie. Clearly, with a larger sample, the precision of estimation of the population exponent would improve. In the current study, the precision (confidence interval half-width) for the common muscle volume exponent was 0.24. If a much greater precision were desired (for example, 0.1) the sample size requirements would be inflated approximately five-fold. However, given that our primary aim was to shed light on the most appropriate body size denominator for the scaling of \( \dot{V}O_2 \) max – rather than to define the precise population value of the exponent - the cost: benefit ratio of a much larger study would seem high. We believe, therefore, that our sample size is adequate for addressing the specific research question posed.

In conclusion, in a heterogeneous sample of boys and men, we have demonstrated clearly that an estimate of a proportion of the involved musculature is a more valid allometric scaling denominator than either BM or FFM, for properly partitioning out the influence of body size on \( \dot{V}O_2 \) max. Further research is required, quantifying a larger proportion of active muscle that is utilised during exercise, to confirm our findings.
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REFERENCES


LEGENDS

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Table 3  The relationship between power function ratios ($Y/X^b$) and individual body size scaling denominators (X) by group
Figure 1  The relationship between fat free mass (FFM) and the ratio of muscle volume (VOL) to FFM
Table 1  Physical and physiological characteristics

<table>
<thead>
<tr>
<th>Variable</th>
<th>Boys (n = 15)</th>
<th>Men (n = 14)</th>
<th>Alpha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (y)*</td>
<td>12.3 (0.3)</td>
<td>25.4 (4.4)</td>
<td>0.000</td>
</tr>
<tr>
<td>Stature (m)*</td>
<td>1.54 (0.09)</td>
<td>1.81 (0.06)</td>
<td>0.000</td>
</tr>
<tr>
<td>Body mass (kg)*</td>
<td>43.6 (6.8)</td>
<td>78.3 (10.9)</td>
<td>0.000</td>
</tr>
<tr>
<td>Body fat (%)</td>
<td>14.8 (4.6)</td>
<td>15.9 (4.4)</td>
<td>0.506</td>
</tr>
<tr>
<td>Fat free mass (kg)*</td>
<td>37.0 (5.5)</td>
<td>65.6 (7.9)</td>
<td>0.000</td>
</tr>
<tr>
<td>Muscle volume (mL)*</td>
<td>1057 (251)</td>
<td>2023 (288)</td>
<td>0.000</td>
</tr>
<tr>
<td>Peak heart rate (beats·min⁻¹)*</td>
<td>202 (7)</td>
<td>195 (7)</td>
<td>0.014</td>
</tr>
<tr>
<td>Peak respiratory exchange ratio*</td>
<td>1.09 (0.08)</td>
<td>1.16 (0.03)</td>
<td>0.004</td>
</tr>
<tr>
<td>Maximal oxygen uptake (mL·min⁻¹)*</td>
<td>2229 (371)</td>
<td>4102 (580)</td>
<td>0.000</td>
</tr>
</tbody>
</table>

All values are mean(SD)

*Significant between age group difference
Table 2  Allometric modeling of \( \dot{V}O_2 \) max for the body size variables

<table>
<thead>
<tr>
<th>Scaling variable</th>
<th>Group</th>
<th>( \beta )</th>
<th>95% CI</th>
<th>( R^2 )</th>
<th>SEE (L min(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Boys</td>
<td>0.96</td>
<td>0.67 to 1.25</td>
<td>0.80</td>
<td>0.17</td>
</tr>
<tr>
<td>Body mass (kg)</td>
<td>Men</td>
<td>0.73</td>
<td>0.29 to 1.17</td>
<td>0.54</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>0.79</td>
<td>0.53 to 1.06</td>
<td>0.92</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td>Boys</td>
<td>1.00</td>
<td>0.76 to 1.25</td>
<td>0.86</td>
<td>0.14</td>
</tr>
<tr>
<td>Fat free mass (kg)</td>
<td>Men</td>
<td>0.99</td>
<td>0.61 to 1.38</td>
<td>0.74</td>
<td>0.30</td>
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<tr>
<td></td>
<td>Combined</td>
<td>1.00</td>
<td>0.78 to 1.22</td>
<td>0.95</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>Boys</td>
<td>0.62</td>
<td>0.42 to 0.82</td>
<td>0.77</td>
<td>0.18</td>
</tr>
<tr>
<td>Muscle volume (mL)</td>
<td>Men</td>
<td>0.65</td>
<td>0.18 to 1.12</td>
<td>0.44</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>0.64</td>
<td>0.40 to 0.88</td>
<td>0.91</td>
<td>0.32</td>
</tr>
</tbody>
</table>

Independent Group Model: \( \dot{V}O_2 \) max = \( a \cdot X^b \) (for boys or men)

Combined Group Model: \( \dot{V}O_2 \) max = \( a \cdot X^b \cdot \exp(c \cdot \text{group}) \)

(where \( \beta \) denotes the scaling exponent (b) derived from the regression model; CI are the 95% confidence intervals for \( \beta \); \( R^2 \) is the adjusted coefficient of determination; SEE is the standard error of the estimate, derived from the standard deviation of the model residuals, with the appropriate correction for degrees of freedom).
Table 3  The relationship (95% confidence interval, CI) between power function ratios $(Y/X^b)$ and individual body size scaling denominators $(X)$ by group

<table>
<thead>
<tr>
<th>Scaling Denominator</th>
<th>Boys (n = 15)</th>
<th>Men (n = 14)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>r</td>
<td>95% CI</td>
</tr>
<tr>
<td>Body mass</td>
<td>0.33</td>
<td>-0.22 to 0.72</td>
</tr>
<tr>
<td>Fat free mass</td>
<td>0.13</td>
<td>-0.41 to 0.6</td>
</tr>
<tr>
<td>Muscle volume</td>
<td>-0.04</td>
<td>-0.54 to 0.48</td>
</tr>
</tbody>
</table>
Figure 1  The relationship between fat free mass (FFM) and the ratio of muscle volume (VOL) to FFM

\[ y = 0.3366x + 15.844 \]
\[ R^2 = 0.3548 \]

\[ y = -0.0112x + 31.602 \]
\[ R^2 = 0.0013 \]