

# UC Irvine

## UC Irvine Previously Published Works

### Title

Calf muscle cross-sectional area and peak oxygen uptake and work rate in children and adults

### Permalink

<https://escholarship.org/uc/item/6q69q83x>

### Journal

American Journal of Physiology, 267(3)

### ISSN

0002-9513

### Authors

Zanconato, S  
Riedy, G  
Cooper, DM

### Publication Date

1994-09-01

### DOI

10.1152/ajpregu.1994.267.3.r720

### Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

# Calf muscle cross-sectional area and peak oxygen uptake and work rate in children and adults

STEFANIA ZANCONATO, GERARD RIEDY, AND DAN M. COOPER

*Division of Respiratory and Critical Care, Department of Pediatrics and Department of Radiology, Harbor-University of California Los Angeles Medical Center, Torrance, California 90509*

**Zanconato, Stefania, Gerard Riedy, and Dan M. Cooper.** Calf muscle cross-sectional area and peak oxygen uptake and work rate in children and adults. *Am. J. Physiol.* 267 (Regulatory Integrative Comp. Physiol. 36): R720–R725, 1994.—It is often assumed that the inherent peak muscle metabolic capacity scales in direct proportion to muscle cross-sectional area and is the same in small and large animals (A. V. Hill. *Sci. Prog.* 38: 208–230, 1950). We wondered whether this relationship between size and function was true during the period of growth and development in humans. Magnetic resonance imaging (MRI) was used to determine calf muscle cross-sectional area (CSA) in 20 children (6–11 yr old, 11 boys) and in 18 adults (23–42 yr old, 10 men). Progressive cycle ergometer exercise was performed to determine peak oxygen uptake ( $\dot{V}O_{2\text{peak}}$ ) and work rate ( $WR_{\text{peak}}$ ). The scaling factor (determined by allometric analysis) relating maximal  $O_2$  uptake ( $\dot{V}O_{2\text{max}}$ ) to muscle CSA for the whole sample population was  $1.04 \pm 0.12$  (SE), but the scaling factor relating  $WR_{\text{peak}}$  to muscle CSA was significantly greater ( $1.37 \pm 0.12$ ). Consistent with this,  $\dot{V}O_{2\text{max}}/CSA$  was not affected by body weight, but the  $WR_{\text{peak}}/CSA$  increased as a function of weight both in males ( $P < 0.005$ ) and females ( $P < 0.05$ ). No differences in  $\dot{V}O_{2\text{max}}/CSA$  were found between children and adults.  $WR_{\text{peak}}/CSA$  was significantly higher in adults compared with children ( $P < 0.05$ ). It appears that the inherent peak muscle metabolic capacity is smaller in children than in adults. Moreover, the coupling of muscle capacity with whole body metabolic rate changes during growth in humans.

magnetic resonance imaging; scaling; allometry

BODY SIZE IS a major determinant of maximal physiological function, and allometric equations quantify the relationships of body size (e.g., muscle mass) to metabolic rate [e.g., peak oxygen uptake ( $\dot{V}O_{2\text{peak}}$ ) during exercise]. Allometric analyses are used to assess size-structure relationships in mature animals of different sizes and species (29) as well as in a single species during the period of growth and development (4, 6, 26, 27). The objective of this study was to examine the relationship between muscle size and the  $\dot{V}O_{2\text{peak}}$  and peak work rate ( $WR_{\text{peak}}$ ) in a group of children and adults.

$\dot{V}O_{2\text{peak}}$  and  $WR_{\text{peak}}$  were measured from a progressive cycle ergometer test. Muscle size was estimated using magnetic resonance imaging (MRI) of the calf musculature. MRI is a noninvasive method not requiring ionizing radiation and is, therefore, more feasible for studies in healthy children. MRI provided a means to measure muscle cross-sectional area (CSA) and allowed us to account for bone and subcutaneous fat, factors that substantially limit the accuracy of limb diameter alone in estimating muscle size.

Allometric equations have the general form

$$q \propto a \cdot M^b$$

where  $q$  indicates a metabolic rate (e.g.,  $\dot{V}O_2$ ),  $M$  is a parameter related to body dimension (e.g., mass),  $a$  is the mass coefficient, and  $b$  is the dimensionless mass exponent or the scaling factor (16). The scaling factor relating body mass to  $\dot{V}O_{2\text{peak}}$  in mature mammals of different sizes is  $\sim 0.75$  (29). In contrast, in cross-sectional studies of children and young adults performed in our laboratory the scaling factor was found to be 1.01 (7), a value significantly greater than 0.75.

The observation of different scaling factors implies that the mechanisms accounting for size-function relationships are not entirely the same during growth in children as among mature animals of different sizes. Hill (18) in 1950 and McMahon (21) in 1984 reviewed the experimental data and theoretical considerations of size-function relationships during exercise in mature animals. Insight into the mechanisms governing size-function relationships during growth can be gained by testing certain assumptions reached by Hill and McMahon

$$\text{Peak muscle function} \propto \text{muscle CSA}^1 \quad (1)$$

The inherent or intrinsic strength of a contracting voluntary muscle fiber is constant and independent of the size of the animal. A bigger muscle is capable of greater work and metabolic rate only because it is bigger, not because its inherent metabolic capacity is greater [Hill (18)].

$$\text{Peak muscle strength} \propto \text{peak metabolic rate} \quad (2)$$

In terms of a progressive exercise test, this could be stated as  $WR_{\text{peak}} \propto \dot{V}O_{2\text{peak}}$ .

These assumptions would then predict that

$$\dot{V}O_{2\text{peak}} \propto \text{muscle CSA}^1$$

and

$$WR_{\text{peak}} \propto \text{muscle CSA}^1$$

We hypothesized that the scaling factor of 1.0, predicted from studies of mature animals, would not be found experimentally in children and adults. An important implication of finding a scaling factor other than 1 would be that the intrinsic strength and/or metabolic capacity of muscles change during growth and development.

## METHODS

**Subjects.** The study population consisted of 20 children (age range: 6–11 yr; 11 boys, 9 girls) and 18 adults (age range 23–42 yr, 10 men, 8 women). Height, weight, and body mass index (BMI = weight/height<sup>2</sup>) are given in Table 1. The mean BMI in the children of this study was virtually identical to the

Table 1. *Anthropometric data: children and adults*

	<i>n</i>	Age, yr	Weight, kg	Height, cm	BMI, kg/m <sup>2</sup>
Boys	11	8.3 ± 1.3	34.1 ± 10.1	137.3 ± 10.8	17.7 ± 3.0
Girls	9	8.4 ± 1.7	31.7 ± 6.7	135.6 ± 8.5	17.3 ± 3.1
All children	20	8.4 ± 1.4	33.0 ± 8.6	136.5 ± 9.6	17.6 ± 3.0
Men	10	32.7 ± 5.1	77.8 ± 12.2	180.2 ± 7.9	23.9 ± 2.4
Women	8	30.9 ± 6.4	58.8 ± 5.2	162.4 ± 7.5	22.4 ± 1.8
All adults	18	31.9 ± 5.6	69.3 ± 13.6	172.3 ± 11.8	23.2 ± 2.3

Values are means ± SD; *n*, no. of subjects. BMI, body mass index (weight/height<sup>2</sup>).

mean BMI in healthy children studied previously in our laboratory [ $17.5 \pm 2.9$  kg/m<sup>2</sup> (SD) from comparably aged subjects (7)]. For the men and women BMI was well within the normal range as recently published (25). All subjects were screened before participation to ensure that none were smokers, suffered from chronic lung or heart disease, were obese, or used drugs or medications on a chronic basis. The study was approved by the Institutional Human Subject's Review Board and informed consent was obtained from each participant and parent or guardian, when appropriate.

**Progressive exercise test.** Each subject performed a ramp-type progressive exercise test on an electromagnetically braked cycle ergometer to determine the maximal oxygen uptake ( $\dot{V}O_{2\max}$ ). A smaller ergometer was used for younger children as previously described (1). This protocol has been used extensively in adults and children to determine gas exchange parameters of exercise, such as the  $\dot{V}O_{2\text{peak}}$  (7, 32).  $\dot{V}O_{2\text{peak}}$  and  $WR_{\text{peak}}$  were determined as the largest  $\dot{V}O_2$  and work rate achieved by each subject during the progressive test in which each subject was vigorously encouraged to achieve maximal efforts. In a previous study of healthy children and young adults (7), we demonstrated that the  $\dot{V}O_{2\text{peak}}$  was virtually indistinguishable from the true  $\dot{V}O_{2\max}$  (i.e., the appearance of a plateau for  $\dot{V}O_2$ ).

**Pulmonary gas exchange.** Pulmonary gas exchange was measured breath by breath. The subjects breathed through a low-impedance turbine volume transducer and a breathing valve with a combined dead space of 90 ml. Mouth  $O_2$  and  $CO_2$  tensions were determined by mass spectrometry from a sample drawn continuously from the mouthpiece at 1 ml/s. The inspired and expired volume and gas fraction signals underwent analog-to-digital conversion, from which  $O_2$  uptake (STPD),  $CO_2$  output (STPD), and minute expired ventilation (BTPS) were calculated on-line with each breath, as previously described (3).

**MRI.** MRI was performed on a Picker 1.5-T whole body MRI System. A 10-cm round surface coil was used for signal detection, while a proton body coil was employed for RF transmission for imaging. The subject was positioned with the center of the receive coil at the largest circumference of the calf (as estimated by the investigator). The whole leg was then moved into the isocenter of the magnet bore. Images were obtained from a 2-cm coronal slice at isocenter with a 30-cm field of view. A gradient echo sequence with a  $256 \times 256$  matrix and two acquisitions at each phase encode step at a time to echo (TE) of 30 ms and repetition time (TR) of 300 ms was employed. These images provided single-slice pictures of muscle, fat, and bone.

**MRI analysis.** An example of an image obtained from an 8-yr-old boy is shown in Fig. 1. Computerized planimetry was used to determine calf muscle CSA. The major muscles included were: gastrocnemius, soleus, tibialis anterior and posterior, and peroneus longus and brevis. The investigator traced the circumference of the calf using a pointing device.

This maneuver was performed three times with a coefficient of variation of 0.7%. As can be seen in Fig. 1, areas of fat and bone were readily recognizable from the MRI. These areas were traced as well and subsequently subtracted from the limb CSA to yield the muscle CSA. A similar approach was recently presented by Nishida and co-workers (22).

**Determination of scaling factor.** A log-log transform was used to calculate the scaling factor (16). Linear regression was performed on the transformed data, and the slope of the regression is equal to the scaling factor. Because work of all of the calf muscles is a major component of the total work done during cycle ergometry (15, 17), we used the ratios of  $\dot{V}O_{2\text{peak}}$  to CSA and  $WR_{\text{peak}}$  to CSA as indicators of the relative contribution of this muscle group to maximal metabolic rate and maximal power output. These ratios were analyzed in several ways: first, we calculated the mean value for the four groups: boys, girls, men, and women. Second, we calculated the linear regression of the ratios as a function of body weight in all male subjects, all female subjects, and in the group as a whole.

**Statistical analysis.** Standard techniques were used to calculate the slopes and *y*-intercepts for best fit linear regressions. The *t* test was used to determine if particular regression coefficients differed significantly from 0 (12). Analysis of variance (ANOVA) was used to compare  $WR_{\text{peak}}/CSA$ ,  $\dot{V}O_{2\text{peak}}/CSA$ , and the spectroscopy parameters among four groups: boys, girls, men, and women. When ANOVA was found to be significant, an appropriately modified *t* test (Duncan) was used for intergroup comparisons. In addition, analysis of covariance (ANCOVA) was used for intergroup comparisons of  $WR_{\text{peak}}$  using muscle CSA as the covariate.

## RESULTS

**Gas exchange.** The mean  $\dot{V}O_{2\text{peak}}$  normalized to body weight was  $39.9 \pm 8.6$  (SD) ml · min<sup>-1</sup> · kg<sup>-1</sup> in the adults and  $38.8 \pm 7.4$  in children (no significant difference). In addition, the  $\dot{V}O_{2\text{peak}}$  as percent predicted [based on normal values in our laboratory (7)] was  $86 \pm 18\%$  in the men,  $112 \pm 28\%$  in the women,  $90 \pm 24\%$  in the boys, and  $103 \pm 15\%$  in the girls (SD). There were no significant differences among the groups. These results suggest, indirectly, that fitness levels were roughly the same in all four groups.

$WR_{\text{peak}}$  per body weight in children ( $2.9 \pm 0.6$  W/kg) was significantly lower than in adults ( $3.9 \pm 0.8$  W/kg,  $P < 0.001$ ). Both  $\dot{V}O_{2\text{peak}}$  and  $WR_{\text{peak}}$  were similar to values found previously in our laboratory (7, 33).

**Scaling factors.** The scaling factors relating  $WR_{\text{peak}}$  and  $\dot{V}O_2$  to muscle CSA are shown in Table 2. Table 3 summarizes the linear regression analysis for  $WR_{\text{peak}}/CSA$  and  $\dot{V}O_{2\text{peak}}/CSA$  as a function of body weight in males, females, and in the group as a whole.  $\dot{V}O_{2\text{peak}}/CSA$  was not affected by body weight, but the  $WR_{\text{peak}}/CSA$  increased as a function of weight both in males ( $P < 0.005$ ) and females ( $P < 0.05$ ). No differences in  $\dot{V}O_{2\text{peak}}/CSA$  were observed between children and adults. On the contrary,  $WR_{\text{peak}}/CSA$  was significantly higher in adults compared with children (Fig. 2).

**ANCOVA results.** Table 4 summarizes the means and adjusted means for  $WR_{\text{peak}}$  with muscle CSA as a covariate. The results of this analysis also indicated that  $WR_{\text{peak}}$  was significantly greater in the men compared with all other groups. In addition,  $WR_{\text{peak}}$  in women was greater than  $WR_{\text{peak}}$  in the boys and girls.

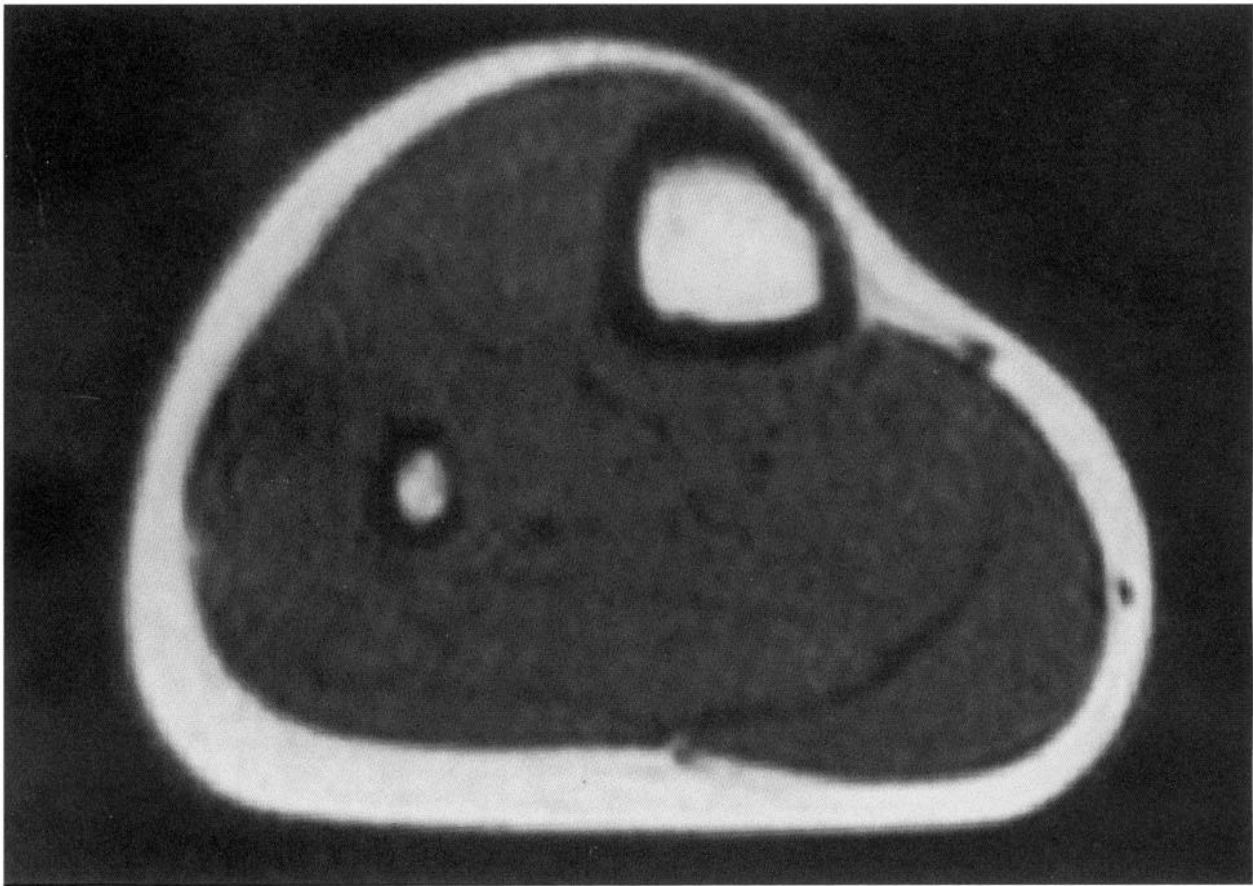


Fig. 1. Magnetic resonance imaging of the right calf muscle area in an 8-yr-old girl.

## DISCUSSION

We found, as expected, that  $WR_{\text{peak}}$ ,  $\dot{V}O_{2\text{peak}}$ , and calf muscle CSA all increased with age and body size in this group of children and adults. As hypothesized, the scaling factor relating  $WR_{\text{peak}}$  to muscle CSA was significantly greater than 1.0 (Table 2). This was corroborated by the ANCOVA results and the observations that the ratio  $WR_{\text{peak}}/CSA$  increased significantly with body weight, and that the mean values of  $WR_{\text{peak}}/CSA$  were less in boys and girls than in men and women (Fig. 2). A possible implication of this finding is that inherent muscle metabolic capacity increases with size during growth and maturation.

But we had also hypothesized that the scaling factors for both  $\dot{V}O_{2\text{peak}}$  and  $WR_{\text{peak}}$  to muscle CSA would be the same, since  $WR_{\text{peak}} \propto \dot{V}O_{2\text{peak}}$  (assumption 2). This was not the case: the scaling factor of  $\dot{V}O_{2\text{peak}}$  to muscle CSA did not significantly differ from 1.0. This was corroborated by the observation that the ratio  $\dot{V}O_{2\text{peak}}/CSA$  did

not change with body weight. One implication of the discrepancy between the  $WR_{\text{peak}}$  and  $\dot{V}O_{2\text{peak}}$  scaling factors is that the coupling of  $\dot{V}O_2$  (measured at the mouth) to muscle work and metabolic rate may change during growth and maturation.

It is first necessary to address some of the methodologic limitations of this study. Working with children imposes a number of real constraints: these subjects, while enthusiastic and cooperative, can become distracted rather quickly, particularly in the confines of a whole body magnet, and start moving and fidgeting. Thus images must be obtained quickly. We chose to

Table 3. Linear regression analysis for  $WR_{\text{peak}}/CSA$  and  $\dot{V}O_{2\text{peak}}/CSA$  as a function of body wt

	Slope	Constant	<i>r</i>	<i>P</i> Value
$WR_{\text{peak}}/CSA$ , male	0.043	2.34	0.70	<0.005
$WR_{\text{peak}}/CSA$ , female	0.045	2.17	0.57	<0.05
$WR_{\text{peak}}/CSA$ , all	0.044	2.26	0.68	<0.0001
$\dot{V}O_{2\text{peak}}/CSA$ , male	0.13	47.2	0.24	NS
$\dot{V}O_{2\text{peak}}/CSA$ , female	0.18	41.3	0.25	NS
$\dot{V}O_{2\text{peak}}/CSA$ , all	0.17	43.6	0.29	NS

Regression slope and constant for the equation:  $y = a \cdot x + b$ , where  $y$  is either  $WR_{\text{peak}}/CSA$  or  $\dot{V}O_{2\text{peak}}/CSA$ ,  $a$  is the slope either as  $W \cdot \text{cm}^{-2} \cdot \text{kg}^{-1}$  or  $\text{ml} \cdot \text{min}^{-1} \cdot \text{cm}^{-2} \cdot \text{kg}^{-1}$ ,  $x$  is body weight in kg, and  $b$  is the constant in either  $W/\text{cm}^2$  or  $\text{ml} \cdot \text{min}^{-1} \cdot \text{cm}^{-2}$ .  $r$ , Correlation coefficient;  $P$  values are calculated for significance of the difference of the slope from the value 0.

Table 2. Scaling factors relating indexes of body mass with metabolic function during exercise

	Females	Males	All Subjects
$WR_{\text{peak}}$ vs. CSA	$1.25 \pm 0.22$	$1.40 \pm 0.16$	$1.37 \pm 0.12$
$\dot{V}O_{2\text{peak}}$ vs. CSA	$0.94 \pm 0.21$	$1.03 \pm 0.15$	$1.04 \pm 0.12$

Values are means  $\pm$  SE.  $WR_{\text{peak}}$ , peak work rate;  $\dot{V}O_{2\text{peak}}$ , peak oxygen uptake; CSA, cross-sectional area.

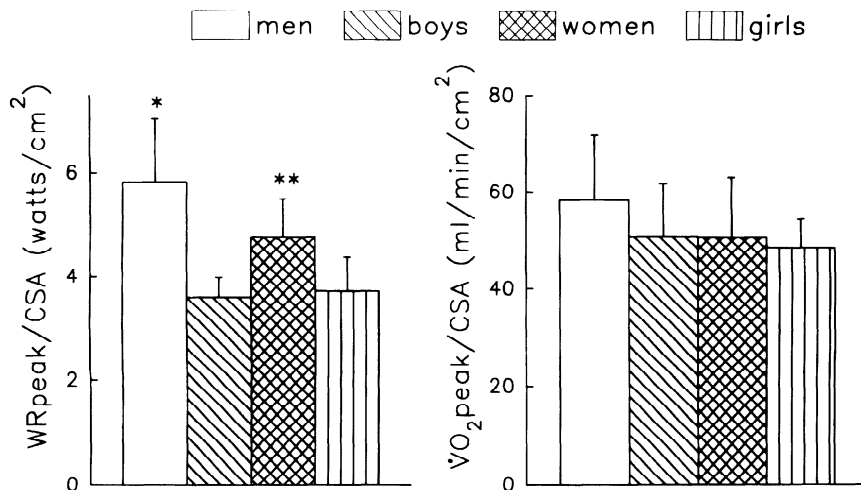


Fig. 2. Peak work rate ( $WR_{peak}$ )/cross-sectional area (CSA) and peak oxygen uptake ( $\dot{V}O_{2peak}$ )/CSA in adults (males and females) and children (boys and girls). \* $WR_{peak}/CSA$  in men was significantly greater than in boys ( $P < 0.05$ ) and girls ( $P < 0.05$ ). \*\* $WR_{peak}/CSA$  in women was significantly greater than in boys ( $P < 0.05$ ). No differences were found in  $\dot{V}O_{2peak}/CSA$  among the 4 groups. Data are expressed as means  $\pm$  SD.

image the calf muscle simply because the investigator could easily and quickly identify the prominent gastrocnemius head, which invariably represents the largest diameter of the lower leg. It is important to reiterate that electromyographic studies have demonstrated that work of the calf muscles is a major component of the total work done during cycle ergometry (15, 17).

Tanner (28) and Toth and co-workers (30) have argued that the use of ratios to compare size-function relationships among different populations may lead to spurious results and suggested the use of ANCOVA to mitigate this problem. In the present study, both the ANCOVA approach and the analysis of ratios led to similar conclusions about the relationship between  $WR_{peak}$  and calf muscle CSA in children and adults. In addition, the power analysis of the data and the analysis of ratios were consistent and also led to the same conclusions. Thus while it is beyond the scope of this paper to deal with the statistical and mathematical objections raised by Tanner and by Toth and co-workers, our results appear to be robust and amenable to a variety of analytic approaches.

An inherent assumption of this study is that the calf muscle CSA accurately represents all muscles involved in ergometry exercise. The calf muscles (e.g., soleus and gastrocnemius) are used extensively in cycle ergometry and have electromyographic power spectra during cycle ergometry similar to the vastus medialis of the thigh musculature (15, 17), but our results cannot exclude the possibility that the recruitment of thigh and calf muscles in cycle ergometer actually changes with age. For example, if children relied on thigh muscles to a greater

extent than did adults in the performance of heavy cycle ergometer exercise, then our results could be explained without necessarily concluding that muscle power per CSA is smaller in children than in adults.

The relative inability of MRI to identify intramuscular fat could also add to the error of this technique. If the muscle CSA in children reflected a higher fat-to-muscle ratio than adults, then the  $WR_{peak}/CSA$  ratio would likely be lower in children and not necessarily indicate differences in muscle tissue per se. We did not measure lean body mass per se, but we used the BMI (Table 1) to estimate %body fat using the equations developed by Deurenberg and co-workers (10). These equations are different in adults and children, reflecting the effect of maturation on the relationship between BMI and %body fat. For the men, the calculated %body fat was 20%, while for the boys the value was 19%; for the women and girls the predicted values were 29 and 22%, respectively. Thus the children were certainly not relatively fatter, and, in the case of the females, were somewhat leaner than the adults. If anything, an inability to account for intramuscular fat by MRI would mean that we had underestimated the true difference in  $WR_{peak}/CSA$  between adults and children.

As noted, we chose the calf because the prominence of the gastrocnemius head makes it relatively easy to choose the largest circumference by inspection. But using only a single CSA could lead to possible errors due to position of the coil or maturational changes in the calf muscle anatomy. MRI may yield other ways of assessing muscle size that could potentially improve this type of analysis. For example, Roman and co-workers (24) recently showed increases in muscle size in elderly men after upper arm resistance training by using 1-cm contiguous MRI-derived CSA and calculating the volume of the muscle in question. In addition, Kuno and co-workers (19) recently demonstrated that MRI techniques can be used to noninvasively assess muscle fiber types. If demonstrated to be applicable for children, then these techniques might provide noninvasive tools to follow maturation of muscles during growth in children.

Despite these possible confounding features of the methodology, our observations are consistent with previ-

Table 4. Means and ANCOVA-adjusted means for  $WR_{peak}$  with CSA as covariate in the 4 groups of subjects

Group	Mean $WR_{peak}$ , W	ANCOVA-Adjusted Mean $WR_{peak}$ , W	SE
Men	331	283*	25
Boys	97	131	23
Women	207	198†	18
Girls	96	133	23

\*Men greater than all other groups ( $P < 0.006$ ); †women greater than girls and boys ( $P < 0.05$ ).

ous studies focused on different aspects of muscle function. From our own laboratory, reanalysis of previous progressive exercise data in a large number of children and teenagers revealed that the ratio of  $WR_{\text{peak}}$ /kilogram body weight increased with age in children and teenagers (7, 33). This was unexpected, since *assumptions 1* and *2* above would suggest that  $WR_{\text{max}} \propto \text{weight}^{2/3}$ , and, therefore, that the ratio of  $WR_{\text{max}}$ /weight would decrease as body weight increased (APPENDIX). Davies and co-workers (8) measured electrically evoked contractile properties of the triceps surae muscle in children and adults. They calculated the mean force per cross-sectional area (estimated by anthropometry and water displacement) to be greater in young adults (34 N/cm<sup>2</sup>) than in children (29 N/cm<sup>2</sup>), even though the children in their study were not as young (mean age 13 years) as in our study. Finally, Parker and co-workers (23) found that isometric quadriceps strength in boys and male teenagers increased even when growth in height and body weight had virtually ceased.

Very little is known about the anatomic and/or biochemical maturation of muscles postnatally in humans. As would be expected, there are very few invasive studies of skeletal muscle fiber types in healthy children, but the work of Bell et al. (5) showed no obvious histological differences between 6-yr-old children and adults. However, there is evidence from other human and animal studies that muscle maturation does occur. Eriksson et al. (13) reported a lower muscle concentration of phosphofructokinase in 11- to 13-yr-old children compared with adults. Studies in rats showed a 17-fold increase in total PFK activity occurring during the first 2 mo of age (equivalent to birth to puberty in humans). This was accompanied by a dramatic decrease in C-type PFK subunit and increase in M-type subunit, the isozyme best suited for glycolysis (11), presumably facilitating anaerobic metabolism.

Along these lines, Bar-Or and others (2, 14) have suggested that there is an increasing anaerobic capacity (the ability to effect ATP regeneration for muscular work anaerobically) as children mature into adulthood. Whether or not such changes are related to the anabolic effects of puberty is not known; however, it is noteworthy that the increases in  $WR_{\text{peak}}/\text{CSA}$  were observed in both males and females. To the extent that our observations can be explained by hormonal changes occurring during the process of maturation, the role of both estradiol and testosterone, the hormones responsible for the female and male adolescent growth spurts (20), must be considered.

As noted, unlike the  $WR_{\text{peak}}$ , the  $\dot{V}O_{2\text{peak}}$  increased in direct proportion with muscle CSA: the scaling factor was not significantly different from 1.0. Davies and co-workers (9) discovered that  $\dot{V}O_{2\text{peak}}$ , when scaled to leg volume (determined by anthropometry and water displacement), actually decreased slightly with increasing age in a cross-sectional study of children and adults. Moreover, in previous studies in this laboratory we found that the oxygen cost of 1 min of high-intensity exercise, normalized to external work performed ( $\text{ml} \cdot \text{min}^{-1} \cdot \text{J}^{-1}$ ), was actually greater in children compared with adults (33).

Maturation of the "anaerobic potential" referred to above may shed light on the apparent discrepancy between  $WR_{\text{peak}}$  and  $\dot{V}O_{2\text{peak}}$ . The  $\dot{V}O_2$  during exercise does not necessarily represent the total metabolic cost of the work performed. In particular, ATP rephosphorylation derived from anaerobic metabolism and from high-energy phosphagen stores, important components of the total metabolic cost of exercise (31), is simply not accounted for by gas exchange measured at the mouth. Our data may be explained by the following scenario: muscles grow in size and gain potential for anaerobic metabolism as children grow and develop.  $WR_{\text{peak}}$  increases out of proportion to the growth in muscle (i.e., the scaling factor for  $WR_{\text{peak}}$  and muscle CSA is  $> 1.0$ ), but a greater proportion of the energy required to perform the work is anaerobically derived, not reflected in the  $\dot{V}O_{2\text{peak}}$ . Consequently, as muscles become bigger,  $WR_{\text{peak}}$  scales differently with respect to muscle size than does the  $\dot{V}O_{2\text{peak}}$ .

These observations support the notion that the relationship between body size and function during growth is not the same as in mature animals. Moreover, some of the assumptions often used in allometric analyses of size-function relationships during exercise do not appear to hold when the size changes that occur during normal growth and development are considered. Our data suggest that the inherent peak muscle metabolic capacity increases with age in human beings.

#### APPENDIX

$$\text{muscle CSA} \propto l^2$$

where  $l$  (length) is a linear dimension of body size, and

$$\text{body weight} \propto \text{body volume} \propto l^3$$

then

$$\text{weight} \propto \text{muscle CSA}^{2/3}$$

Finally, if

$$WR_{\text{max}} \propto \text{muscle CSA}^1 \text{ (assumption 1)}$$

then

$$WR_{\text{max}} \propto \text{weight}^{2/3}$$

---

S. Zanconato was a Research Fellow of the American Heart Association, Greater Los Angeles Affiliate. D. M. Cooper is a recipient of the Career Investigator Award of the American Lung Association.

This work was supported by National Heart, Lung, and Blood Institute Grant HD-26939-02 and a grant from the American Diabetes Association.

Address for reprint requests: D. M. Cooper, Harbor-UCLA Medical Center, N-4, 1000 West Carson St., Torrance, CA 90509.

Received 10 November 1993; accepted in final form 22 March 1994.

#### REFERENCES

1. Armon, Y., D. M. Cooper, R. Flores, S. Zanconato, and T. J. Barstow. Oxygen uptake dynamics during high-intensity exercise in children and adults. *J. Appl. Physiol.* 70: 841-848, 1991.
2. Bar-Or, O. *Pediatric Sports Medicine for the Practitioner*. New York: Springer-Verlag, 1983.
3. Beaver, W. L., N. Lamarra, and K. Wasserman. Breath-by-breath measurement of true alveolar gas exchange. *J. Appl. Physiol.* 51: 1662-1675, 1981.
4. Belk, K. E., J. D. Tatum, and F. L. Williams, Jr. Deposition and distribution of carcass fat for steers differing in frame size and muscle thickness. *J. Anim. Sci.* 69: 609-616, 1991.
5. Bell, R. D., J. D. MacDougall, R. Billeter, and H. Howald. Muscle fiber types and morphometric analysis of skeletal muscle in six-year-old children. *Med. Sci. Sports Exercise* 12: 28-31, 1980.

6. **Cooper, D. M.** Development of the oxygen transport system in normal children. In: *Advances in Pediatric Sport Sciences: Biological Issues*, edited by O. Bar-Or. Champaign, IL: Human Kinetics Books, 1989, vol. 3, p. 67–100.
7. **Cooper, D. M., D. Weiler-Ravell, B. J. Whipp, and K. Wasserman.** Aerobic parameters of exercise as a function of body size during growth in children. *J. Appl. Physiol.* 56: 628–634, 1984.
8. **Davies, C. T. M., M. J. White, and K. Young.** Muscle function in children. *Eur. J. Appl. Physiol. Occup. Physiol.* 52: 111–114, 1983.
9. **Davies, D. T. M., C. Barnes, and S. Godfrey.** Body composition and maximal exercise performance in children. *Hum. Biol.* 44: 195–214, 1972.
10. **Deurenberg, P., J. A. Weststrate, and J. C. Seidell.** Body mass index as a measure of body fatness: age- and sex-specific prediction formulas. *Br. J. Nutr.* 65: 105–114, 1991.
11. **Dunaway, G. A., T. P. Kasten, G. A. Nickols, and J. A. Chesky.** Regulation of skeletal muscle 6-phosphofructo-1-kinase during aging and development. *Mech. Ageing Dev.* 36: 13–23, 1986.
12. **Edwards, A. L.** *An Introduction to Linear Regression and Correlation.* San Francisco, CA: Freeman, 1976, p. 103–113.
13. **Eriksson, B. O., P. B. Gollnick, and B. Saltin.** Muscle metabolism and enzyme activity after training in boys 11–13 years old. *Acta Physiol. Scand.* 87: 485–487, 1973.
14. **Falk, B., and O. Bar-Or.** Longitudinal changes in peak aerobic and anaerobic mechanical power of circumpubertal boys. *Pediatr. Exer. Sci.* 5: 318–331, 1993.
15. **Gamet, D., J. Duchene, C. Garapon Bar, and F. Goubel.** Electromyogram power spectrum during dynamic contractions at different intensities of exercise. *Eur. J. Appl. Physiol. Occup. Physiol.* 61: 331–337, 1990.
16. **Gould, S. J.** Allometry and size in ontogeny and physiology. *Biol. Rev. Camb. Philos. Soc.* 41: 587–640, 1966.
17. **Hanninen, O., O. Airaksinen, M. Karipohja, K. Manninen, T. Sihvonen, and H. Pekkarinen.** On-line determination of anaerobic threshold with rms-EMG. *Biomed. Biochim. Acta* 48: S493–S503, 1989.
18. **Hill, A. V.** The dimensions of animals and their muscular dynamics. *Sci. Prog.* 38: 208–230, 1950.
19. **Kuno, S., S. Katsuta, M. Akisada, I. Anno, and K. Matsu-moto.** Effect of strength training on the relationship between magnetic resonance relaxation time and muscle fibre composition. *Eur. J. Appl. Physiol. Occup. Physiol.* 61: 33–36, 1990.
20. **Marshall, W. A., and J. M. Tanner.** Puberty. In: *Human Growth*, edited by F. Falkner and J. M. Tanner. New York: Plenum, 1986, p. 171–210.
21. **McMahon, T. A.** *Muscles, Reflexes, and Locomotion.* Princeton, NJ: Princeton Univ. Press, 1984.
22. **Nishida, M., H. Nishijima, K. Yonezawa, I. Sato, T. Anzai, K. Okita, and H. Yasuda.** Phosphorus 31 magnetic resonance spectroscopy of forearm flexor muscles in student rowers using an exercise protocol adjusted for differences in cross-sectional muscle area. *Eur. J. Appl. Physiol. Occup. Physiol.* 64: 528–533, 1992.
23. **Parker, D. F., J. M. Round, P. Sacco, and D. A. Jones.** A cross-sectional survey of upper and lower limb strength in boys and girls during childhood adolescence. *Ann. Hum. Biol.* 17: 199–211, 1990.
24. **Roman, W. J., J. Fleckenstein, J. Stray-Gundersen, S. E. Alway, R. Peshock, and W. J. Gonyea.** Adaptations in the elbow flexors of elderly males after heavy-resistance training. *J. Appl. Physiol.* 74: 750–754, 1993.
25. **Rowland, M. L.** A nomogram for computing body mass index. *Dietetic Currents* 16: 5–12, 1989.
26. **Siddiqui, R. A., S. N. McCutcheon, H. T. Blair, D. D. Mackenzie, P. C. Morel, B. H. Breier, and P. D. Gluckman.** Growth allometry of organs, muscles and bones in mice from lines divergently selected on the basis of plasma insulin-like growth factor-I. *Growth Dev. Aging* 56: 53–60, 1992.
27. **Sjodin, B., and J. Svedenhag.** Oxygen uptake during running as related to body mass in circumpubertal boys: a longitudinal study. *Eur. J. Appl. Physiol. Occup. Physiol.* 65: 150–157, 1992.
28. **Tanner, J. M.** Fallacy of per-weight and per-surface area standards and their relation to spurious correlation. *J. Appl. Physiol.* 2: 1–15, 1949.
29. **Taylor, C. R., G. M. O. Maloiy, E. R. Weibel, V. A. Langman, J. M. Z. Kamau, H. J. Seeherman, and N. C. Heglund.** Design of the mammalian respiratory system: 3. Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respir. Physiol.* 44: 25–38, 1981.
30. **Toth, M. J., M. I. Goran, P. A. Ades, D. B. Howard, and E. T. Poehlman.** Examination of data normalization procedures for expressing peak  $\dot{V}O_2$  data. *J. Appl. Physiol.* 75: 2288–2292, 1993.
31. **Wasserman, K., B. J. Whipp, and J. A. Davis.** Respiratory physiology of exercise: metabolism, gas exchange, and ventilatory control. In: *Respiratory Physiology III*, edited by J. G. Widdicombe. Baltimore, MD: University Park, 1981, vol. 23, p. 150–211. (Int. Rev. Physiol. Ser.)
32. **Whipp, B. J., J. A. Davis, F. Torres, and K. Wasserman.** A test to determine parameters of aerobic function during exercise. *J. Appl. Physiol.* 50: 217–221, 1981.
33. **Zanconato, S., D. M. Cooper, and Y. Armon.** Oxygen cost and oxygen uptake dynamics and recovery with one minute of exercise in children and adults. *J. Appl. Physiol.* 71: 993–998, 1991.