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Original article

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DECLARATIONS

Author contribution statement

HM, CT and SR designed the research. JB, AD, HM, CT and SR collected the data and performed the research. JB, AD, NA and SR analysed the data and supervised the research. JB and SR wrote the manuscript. JB, HM, AD, NA, CT and SR provided critical revisions important for intellectual content of the finished manuscript, approved the final version of the manuscript, and agree to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

Ethics approval

The present study was approved by an institutional ethics review board (Comité d'Éthique pour la Recherche en Sciences et Techniques des Activités Physiques et Sportives – CERSTAPS, n°2019-18-09-36) and conformed to the standards of use of human participants in research as outlined in the *Sixth Declaration of Helsinki*.

Consent to participate

Written informed consent was obtained from all individual included in the study, and from their parents or legal guardians.

Consent for publication

Participants (and their parents or legal guardians) signed informed consent regarding publishing their data.

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Conflict of interest

The authors declare no competing interests. The results of the study are presented clearly, honestly and without fabrication, falsification or inappropriate data manipulation.

ABSTRACT

Purpose: The aims of the present study were to determine during childhood and adolescence (i) the effect of sex on non-oxidative energy production, quantified by the accumulated oxygen deficit (AOD), and (ii) the influence of AOD on high-intensity performance.

Methods: Thirty-nine boys and 35 girls aged 10-17 years performed a 60-s all-out test on a rowing ergometer to determine AOD and mean power output (MPO). Multiplicative allometric modelling was used to assess the concurrent effects of lean body mass (LBM) and age on AOD.

Results: AOD significantly increased with age in both sexes ($p < 0.001$) with boys exhibiting significantly higher AOD than girls from the age of 14 years (10-11.9 yr: 1.9 vs 1.9 L, 12-13.9 yr: 2.4 vs 2.7 L, 14-15.9 yr: 2.8 vs 4.6 L and 16-17.9 yr: 2.9 vs 5.2 L, in girls and boys respectively, $p < 0.001$). However, a sex difference was no longer significant when AOD was analysed using an allometric model including age and LBM ($p = 0.885$). Finally, significant correlations were found between AOD and MPO in boys and girls but with lower evidence in girls ($r^2 = 0.41$ vs. 0.89).

Conclusion: Non-oxidative energy production increased more extensively in boys than girls from the age of 14 years. Age and LBM accounted for the sexual differentiation of AOD during childhood and adolescence. In addition, AOD was found to be a determinant factor of high-intensity performance, more particularly in boys.

KEY WORDS: non-oxidative metabolism; lean body mass; girls; multiplicative allometric modelling; age.

ABBREVIATIONS

ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
AOD	Accumulated oxygen deficit
BM	Body mass
$[HCO_3^-]_{min}$	Minimal blood bicarbonate concentration
$[La]_{max}$	Maximal blood lactate concentration
LBM	Lean body mass
MPO	Mean power output
pH_{min}	Minimal blood pH
$\dot{V}O_{2max}$	Maximal oxygen uptake
$\dot{V}O_{2rest}$	Oxygen uptake at rest

INTRODUCTION

It is well-established that the development of body composition during childhood and adolescence is sex-specific (Baxter-Jones et al. 2003; Wells 2007). Indeed, post-pubertal boys acquire a greater lean body mass (LBM) and less fat mass than post-pubertal girls during late adolescence (Baxter-Jones et al. 2003; Wells 2007). As fat is metabolically inert (Goran et al. 2000), this sexual dimorphism during puberty strongly influences performance during high-intensity exercise. For instance, peak power output (in W) increases significantly in both sexes from childhood into adolescence (Doré et al. 2001; Martin et al. 2003; Armstrong and Welsman 2019a) but from 13-14 years of age boys develop higher peak power output than girls (Blimkie et al. 1988; Armstrong et al. 1997; Martin et al. 2004; Doré et al. 2005; Mikulic and Markovic 2011; Armstrong and Welsman 2019a). Several authors have suggested that these differences in performance between girls and boys from the age of 13-14 years are influenced by non-oxidative energy output in addition to differences in body composition (Malina et al. 2004; Doré et al. 2005). However, while it is well-established that the contribution of non-oxidative metabolism during high-intensity exercise is greater in post- than pre-pubertal boys (Birat et al. 2018; Ratel et al. 2002b, a), no previous study has evaluated non-oxidative energy production during childhood and adolescence with respect to sex, or established any direct relationship between non-oxidative metabolism and performance during high-intensity exercise from childhood into adolescence.

The activity of non-oxidative metabolism can be assessed using several different methods such as muscle biopsy (Eriksson et al. 1971) or phosphorus^{31} magnetic resonance spectroscopy (Tonson et al. 2010). However, for ethical or technological reasons, these techniques have not been used to evaluate the importance of non-oxidative metabolism in the relative development of the performance of girls and boys. Alternatively, blood lactate assays have been used to explore non-oxidative (glycolytic) metabolism during childhood and adolescence, with only one study reporting a lower blood lactate response following maximal exercise in girls compared to boys, from the age of 16 years (Cumming et al. 1985). However, blood lactate concentration must be interpreted cautiously as lactate sampled in blood cannot be assumed to reflect a consistent or direct relationship with muscle lactate production. The physiological relevance of this blood marker to assess non-oxidative energy turnover during high-intensity whole-body exercise is, therefore, highly debatable (Ferguson et al. 2018).

Among other methods, the measurement of accumulated O_2 deficit (AOD) has been found to be a valid technique in adults (Medbø et al. 1988) and children (Naughton and Carlson 1995) to assess non-oxidative energy production during high-intensity, whole-body exercise. However, use of this method with children and adolescents has seldom been reported. To our knowledge, three studies have reported lower AOD, whether expressed in absolute terms or in ratio with body mass (BM) in 9-12-year-old boys than male adolescents or young men (Hebestreit et al. 1998; Leclair et al. 2011; Diry et al. 2020), thereby suggesting an age effect on non-oxidative energy metabolism. Furthermore, while a sex-related difference in AOD of ~15-25% (relative to body dimensions) has been observed in adults (Medbø and Burgers 1990; Weyand et al. 1993; Ramsbottom et al. 1997; Weber and Schneider 2000), no previous study has analysed changes in AOD during childhood and adolescence with respect to sex. No differences in AOD or AOD relative to BM have been reported during high-intensity exercise between 9-11-year-old non-athletic girls and boys (Carlson and Naughton 1993; Naughton and Carlson 1995; Berthoin et al. 2003). In addition, the only study to have analysed the sex-related difference in AOD in 14-15-year-olds showed that trained girls (n = 8) had significantly lower absolute AOD and AOD relative to BM than trained boys (n = 8) when exercising on an inclined treadmill at two constant exercise intensities (120 and 130% of maximal aerobic power) (Naughton et al. 1997). These differences were also found in performance, as running speed was significantly higher in boys than girls at both exercise intensities (Naughton et al. 1997).

Although in previous studies AOD and performance during high-intensity exercise have been occasionally investigated with small samples of girls and boys, a relationship between metabolic and mechanical parameters has not been directly established (Carlson and Naughton 1993; Naughton and Carlson 1995; Naughton et al. 1997). Leclair et al (2011) reported a positive relationship between AOD relative to BM and time to exhaustion during a cycle exercise at 100% of maximal aerobic power in 9-11-year-old boys; however, a similar relationship was not observed in men.

However, interpretation of AOD is likely to have been clouded in previous studies (Carlson and Naughton 1993; Naughton and Carlson 1995; Naughton et al. 1997; Hebestreit et al. 1998; Berthoin et al. 2003; Leclair et al. 2011) by controlling for differences in body size by simply dividing AOD by BM (i.e., ratio scaling). It is well-established that ratio scaling with BM does not create size-free physiological variables during childhood and adolescence (Welsman and Armstrong 2019). Numerous studies have demonstrated the fallacy of ratio scaling physiological variables and it has been compellingly argued that with cross-sectional data, allometric scaling based in log-linear regression with multiple covariates is the method of choice when investigating the development of physiological variables during growth (Nevill and Holder 1995; Welsman and Armstrong 2000, 2019). Furthermore, as fat mass is metabolically inert (Goran et al. 2000), LBM is a more appropriate covariate of physiological variables during exercise than total BM. LBM varies with age (Baxter-Jones et al. 2003), therefore, allometric analyses including both age and LBM as covariates are likely to provide more insights into AOD than ratio scaling with BM. Moreover, it has been recently demonstrated with multiplicative allometric modelling of large, longitudinal data sets of 11-18-year-olds that, in both sexes the most powerful influence on peak aerobic power, peak power output, and mean power output is concurrent changes in age and LBM, as reflected by the combination of BM and skinfold thicknesses (Armstrong and Welsman 2019a, b).

Therefore, the aims of the present study were to determine during childhood and adolescence (i) the effect of sex on changes in non-oxidative metabolism (i.e., AOD) incurred by high-intensity whole-body exercise, and (ii) the importance of AOD on performance with respect to age and sex. We hypothesised that (i) AOD increases more extensively in boys than in girls from the age of 14 years because of the greater gains in boys' LBM, (ii) sex-related differences in AOD are not significant when changes in both age and LBM are taken into account using a multiplicative allometric model, and (iii) non-oxidative energy production (i.e., AOD) is positively associated with performance (i.e., power output) with the relationship weaker in girls due to the smaller increase in their LBM.

MATERIALS AND METHODS

Subjects

Thirty-nine male and thirty-five female rowers aged from 10 to 17 years volunteered to participate in the present study. All participants trained physically two to three times per week with similar training volumes between girls and boys. None of the participants had a family history of cardiovascular disease or was under medication. The present study was approved by an institutional ethics review board (Comité d'Éthique pour la Recherche en Sciences et Techniques des Activités Physiques et Sportives – CERSTAPS, n°2019-18-09-36) and conformed to the standards of use of human participants in research as outlined in the *Sixth Declaration of Helsinki*. The participants were informed of the experimental procedures and gave their written assent before any testing was conducted. In addition, written informed consent was obtained from the parents or legal guardians of the participants.

Experimental design

Volunteers were tested in two experimental sessions separated by at least 48 hours. Participants were instructed not to undertake any strenuous activity during the 24 hours preceding each session. The first session was dedicated to gathering participants' physical characteristics (anthropometric measurements and body composition) and maximal oxygen uptake ($\dot{V}O_{2max}$) assessment. During the second session, the volunteers performed a 60-s all-out test. The two exercise sessions were carried out on a rowing ergometer (Model D, Concept2, Morrisville, VT, USA). The young participants were fully familiarised with the equipment. The computer of the ergometer continuously delivered the power output (in W). The resistance factor was set by the investigators between 100 and 130 according to age, sex, and the expertise level of young rowers. The same resistance factor was kept for both tests. Verbal encouragement was systematically provided by the investigators during each exercise session.

Experimental measurements

Session 1

Anthropometric characteristics and body composition

BM (in kg) was measured using a digital weight scale with a precision of ± 0.01 kg (Seca 899, Seca, Germany). Standing height (in m) was assessed using a stadiometer with a precision of ± 1 mm (Seca 213, Seca, Germany). Skinfold thicknesses were measured at the triceps and subscapular sites using a Harpenden calliper (British Indicators Ltd, St Albans, UK) and the mean value from three reproducible measurements was calculated. The measurements were taken by the same experienced investigator on the right side of the body to reduce variability in the results for girls and boys. Body fat percentage and LBM (in kg) were determined using the equations developed by Slaughter et al. (1988). These equations are specific to sex, ethnicity, and age, and are recommended for assessing body fat and LBM in children 8-18 years of age.

Maximal oxygen uptake test

Each participant performed a progressive test to exhaustion to determine maximal O_2 uptake ($\dot{V}O_{2max}$ in $L \cdot min^{-1}$). The initial power was set between 40 and 80 W during the first five minutes and the power was incremented by 10-30 W every three minutes according to age, sex, and the expertise level of participants. Arterialised capillary blood samples (20 μL) were taken from the earlobe at rest and every step to measure the time course of blood lactate concentration ([La] in $mmol \cdot L^{-1}$). Whole blood [La] was determined enzymatically using a Biosen C-Line Clinic lactate analyser (EFK Diagnostics GmbH, Barleben, Germany).

Oxygen uptake, carbon dioxide output and ventilation were continuously monitored using a breath-by-breath analyser (Quark CPET, Cosmed, Italy). Heart rate was continuously recorded with a heart rate monitor (HRM-Dual, Garmin, Kansas, USA). $\dot{V}O_{2max}$ was considered to be reached during the last step when at least two of the following criteria were met: (i) $\dot{V}O_2$ levelling-off, (ii) maximal respiratory exchange ratio ≥1.1, (iii) maximal heart rate ≥ 95% of the age-predicted maximal heart rate (208.609 – 0.716 · age) (Shargal et al. 2015) and (iv) blood lactate concentration higher than 8 $mmol \cdot L^{-1}$.

Session 2

60-s all-out test

After a standardised 15-min warm-up at about 130-140 $beats \cdot min^{-1}$ and two short sprints (10-s) in the last five minutes, all participants performed a 60-s all-out test. This test was followed by a 10-min sitting recovery. Cardio-respiratory parameters were continuously measured using a breath-by-breath analyzer (Quark CPET, Cosmed, Italy). Capillary arterialised blood samples (80 μL) were drawn from the earlobe and collected after warm-up and at 1-, 3-, 5-, and 8-min post-exercise to measure the time course of pH, bicarbonate ($[HCO_3^-]$ in $mmol \cdot L^{-1}$) and lactate ([La]). Whole blood [La] was determined enzymatically using the same lactate analyser as in the first session while blood pH and $[HCO_3^-]$ were measured by direct potentiometry using an i-STAT® handheld analyser (Abbott Point of Care, Princeton, USA) immediately after collection. The maximal lactate concentration ($[La]_{max}$), the minimal pH value (pH_{min}) and the minimal bicarbonate ions concentration ($[HCO_3^-]_{min}$) were identified. Mean power output (MPO in W) was calculated over the entire test and individual AOD (in L O_2 Eq.) was determined according to the procedure described below.

Measurements and calculations

Accumulated oxygen deficit

AOD was determined by subtracting accumulated O_2 uptake (the measured O_2 uptake integrated over time) from accumulated O_2 demand (the estimated O_2 demand integrated over time). In accordance with Green and Dawson (1996), oxygen demand was extrapolated using the equation of the $\dot{V}O_2$-power output linear regression obtained during the incremental test and considering the individual value of $\dot{V}O_{2rest}$ (i.e., $\dot{V}O_2$ measured during a period of three minutes before the test). The squared Bravais-Pearson correlation coefficients of linear relationships between $\dot{V}O_2$ and power output ranged between 0.92 and 0.99 (mean ± SD: 0.98 ± 0.02). Because the present study concerned all-out exercise, O_2 demand was calculated from instantaneous power output (recorded stroke by stroke) rather than mean power output sustained during exercise (i.e., MPO) as initially proposed by Medbø et al. (1988).

Allometric modelling procedure

As LBM and age may have influenced the capacity to supply non-oxidative energy, we further investigated the influence of these two factors on AOD through a multiplicative allometric model proposed by Nevill and Holder (1994). This procedure considers the influence of LBM and age on AOD as follows:

$$\text{AOD} = \text{LBM}^{b} \cdot \exp\,(a + c \cdot \text{age}) \cdot \varepsilon \qquad \text{(Eq. 1)}$$

where a is the proportionality coefficient, b and c are the scaling factors associated with LBM and age, respectively, and ε is the normally disturbed error. The statistical approach to allometry is to use a multiple logarithmic transformation, as previously done by Carvalho et al. (2012), as follows:

$$\log\,(\text{AOD}) = b \cdot \log\,(\text{LBM}) + a + c \cdot \text{age} + \log \varepsilon \qquad \text{(Eq. 2)}$$

where b and c are the slopes of the multiple linear regression. These slopes are calculated by ordinary multiple regression analysis where b and c are equal to the scaling factors.

Statistical analysis

Statistical procedures were performed using Statistica 8.0 software (Statsoft, Inc., USA). Descriptive statistics were expressed as mean ± standard deviation (SD) by age group (group 1: 10-11.9 yr, group 2: 12-13.9 yr, group 3: 14-15.9 yr, group 4: 16-17.9 yr) and sex, as proposed by Doré et al. (2005). Data were screened for normality of distribution and homogeneity of variances using a Shapiro-Wilk test and the Levene's test, respectively. Two-way ANOVA was used to examine the effects of sex and age group on AOD and for comparative purposes AOD in ratio with BM. When ANOVA revealed a main or interaction significant effect, an HSD Tukey's *post-hoc* test was applied to test the discrimination between means. The effect size and statistical power have also been reported. The effect size was assessed using the partial eta-squared (η^2) and ranked as follows: ~ 0.01 = small effect, ~ 0.06 = moderate effect, ≥ 0.14 = large effect (Cohen 1969). Linear regression models between age, LBM, AOD, and MPO were fitted by the least-squares method by considering boys and girls separately, and the squared Bravais-Pearson determination coefficients (r^2) of these linear regression models were calculated. The linear regressions between age, LBM and AOD were established in order to check the effects of age and LBM on AOD and then justify the use of age and LBM as scaling factors through the multiplicative allometric model. The slopes of relationships between AOD and MPO were compared between girls and boys using an analysis of covariance (ANCOVA). This procedure was done with an adjustment on x-axis (AOD) since estimation error could be greater on AOD than MPO (Brace 1977). The statistical significance level was set at 5% ($p < 0.05$).

RESULTS

Participants' physical and fitness characteristics

Participants' characteristics are described by age group and sex in Table 1. Statistical analysis revealed no significant sex x age group interaction effect for age [$F_{(3, 66)} = 1.29$, $p = 0.28$, $\eta^2 = 0.06$, power = 0.33]. However, there were significant sex x age group interaction effects for height [$F_{(3, 66)} = 4.83$, $p < 0.01$, $\eta^2 = 0.18$, power = 0.89], BM [$F_{(3, 66)} = 6.55$, $p < 0.001$, $\eta^2 = 0.23$, power = 0.96], LBM [$F_{(3, 66)} = 9.29$, $p < 0.001$, $\eta^2 = 0.30$, power = 0.99], and $\dot{V}O_{2max}$ [$F_{(3, 65)} = 8.69$, $p < 0.001$, $\eta^2 = 0.29$, power = 0.99]. No sex-related significant difference was observed for height, BM, LBM and $\dot{V}O_{2max}$ before the age of 14 years. However, between 14.0 and 17.9 years, boys exhibited significantly higher values for height, BM, LBM and $\dot{V}O_{2max}$. Statistical analysis also revealed a significant sex effect for body fat percentage [$F_{(1, 66)} = 175.5$, $p < 0.001$, $\eta^2 = 0.73$, power = 1.00]. Girls displayed significantly higher values of body fat percentage than boys between 10.0 and 17.9 years ($p < 0.01$, at least).

- Please insert Table 1 near here –

Determination coefficients and allometric exponents

Age was positively correlated to LBM in boys ($r^2 = 0.62$, $p < 0.001$) and girls ($r^2 = 0.13$, $p < 0.05$). Age was also positively correlated to AOD in boys ($r^2 = 0.72$, $p < 0.001$) and girls ($r^2 = 0.23$, $p < 0.01$). In addition, LBM was positively associated with AOD in boys ($r^2 = 0.75$, $p < 0.001$) and girls ($r^2 = 0.22$, $p < 0.01$), and with MPO in boys ($r^2 = 0.86$, $p < 0.001$) and girls ($r^2 = 0.47$, $p < 0.001$).

Allometric scaling exponents *a*, *b*, and *c* for AOD obtained from the multiple procedure (i.e., Eq. 1) were -3.99, 1.03, and 0.08 in boys. The corresponding values in girls were -2.62, 0.78, and 0.04, respectively.

Accumulated Oxygen Deficit (AOD)

AOD values are displayed in absolute terms (L O_2 Eq.) and in ratio with BM (mL O_2 Eq.·kg^{-1}BM) as well as with allometric exponents for LBM and age [L O_2 Eq. / (kg $LBM^b \cdot \exp(a + c \cdot \text{age})$)] by age group and sex in Figure 1. Regardless of sex, AOD increased with age whether in absolute [$F_{(3, 66)} = 31.49$, $p < 0.001$, $\eta^2 = 0.59$, power = 1.00] or in ratio with BM [$F_{(3, 66)} = 13.44$, $p < 0.001$, $\eta^2 = 0.38$, power = 0.99]. Two-way ANOVA also revealed a significant sex x age group interaction effect for absolute AOD [$F_{(3, 66)} = 10.84$, $p < 0.001$, $\eta^2 = 0.33$, power = 0.99] and AOD expressed in ratio with BM [$F_{(3, 66)} = 2.79$, $p = 0.05$, $\eta^2 = 0.11$, power = 0.64]. *Post-hoc* tests showed significantly higher values for absolute AOD and

AOD in ratio with BM unit in boys than girls between 14.0 and 17.9 years ($p < 0.001$). However, there was neither a significant age effect [$F_{(3, 66)} = 1.12$, $p = 0.345$, $\eta^2 = 0.05$, power = 0.29] nor a sex x age group interaction effect [$F_{(3, 66)} = 0.22$, $p = 0.885$, $\eta^2 = 0.01$, power = 0.08] for AOD expressed with allometric exponents (LBM and age).

- Please insert Figure 1 near here -

MPO and post-exercise blood responses

Mean power output (MPO) and post-exercise extreme blood responses ($[La]_{max}$, pH_{min}, $[HCO_3^-]_{min}$) are described by age group and sex in Table 2. Two-way ANOVA showed significant sex x age group interaction effects for MPO [$F_{(3, 66)} = 13.4$, $p < 0.001$, $\eta^2 = 0.38$, power = 0.99] and $[La]_{max}$ [$F_{(3, 66)} = 3.78$, $p < 0.05$, $\eta^2 = 0.15$, power = 0.79] but not for blood pH_{min} [$F_{(3, 64)} = 2.0$, $p = 0.11$, $\eta^2 = 0.09$, power = 0.51] and $[HCO_3^-]_{min}$ [$F_{(3, 61)} = 0.34$, $p = 0.799$, $\eta^2 = 0.02$, power = 0.11]. MPO and $[La]_{max}$ significantly increased with increasing age and values were significantly higher between 16.0 and 17.9 years for $[La]_{max}$ ($p < 0.001$) and between 14.0 and 17.9 years for MPO ($p < 0.001$).

- Please insert Table 2 near here -

Relationships between AOD and MPO

The relationships between AOD (L O_2 Eq.) and MPO (W) in boys and girls are displayed in Figure 2. Significant positive relationships were observed between AOD and MPO in boys ($r^2 = 0.89$, $p < 0.001$) and girls ($r^2 = 0.41$, $p < 0.001$). The slopes of relationships between AOD and MPO were not significantly different between both sexes [$F_{(1, 70)} = 2.30$, $p = 0.13$, $\eta^2 = 0.03$, power = 0.32].

- Please insert Figure 2 near here –

DISCUSSION

The purposes of the present study were to determine during childhood and adolescence (i) the effect of sex on changes in non-oxidative metabolism, as quantified by AOD, and (ii) the importance of AOD on performance with respect to age and sex. The main results confirm our hypotheses since boys exhibited significantly higher AOD values than girls from the age of 14 years, regardless of whether AOD was expressed in absolute terms or in ratio with BM. However, when AOD was analysed in relation to LBM and age in a multiplicative allometric model, a significant difference was no longer observed between girls and boys. In addition, AOD was positively associated with mean power output (MPO), but with less evidence in girls because of a smaller change in LBM. These data show, for the first time, the major role of concurrent changes in LBM and age in the sexual differentiation of non-oxidative metabolism during childhood and adolescence. They also show the importance of non-oxidative metabolism on performance during high-intensity whole-body exercise (i.e., MPO) from childhood into adolescence, more particularly in boys. Taken together, the present data provide new insights into the development and aetiology of non-oxidative metabolism and performance during childhood and adolescence, especially in girls who have been largely understudied compared to boys (McManus and Armstrong 2011).

The results of the present study show a significant age effect on AOD suggesting an increase in non-oxidative energy production during childhood and adolescence in both sexes; however, this effect was found to be less evident in girls. This study is the first to establish an age effect on AOD in girls during childhood and adolescence. In the male population, some studies showed a difference in AOD between prepubertal boys and young men; however, these studies were not designed to test the effect of age and employed small sample numbers with a lack of continuity from childhood into adolescence (Hebestreit et al. 1998; Leclair et al. 2011). The results also show sex-related differences in AOD to only be present from the age of 14 years. These results are consistent with previously published studies of AOD in ratio with BM, which showed with small samples no sex differences in AOD between 9-11-year-olds (Carlson and Naughton 1993; Naughton and Carlson 1995; Berthoin et al. 2003) but significantly higher AOD values in boys than girls at 14-15 years (Naughton et al. 1997).

Sex differences in body composition exerted a strong influence on the comparison of AOD between groups. Indeed, when AOD was expressed in ratio with BM, boys exhibited significantly higher AOD values than girls from the age of 14 years. Multiplicative allometric modelling, however, highlighted that when age is considered concurrently with LBM, the difference in AOD between girls and boys decreased ($p = 0.885$) with age having a greater effect on AOD in boys than girls (c: 0.08 vs. 0.04, respectively). Moreover, when age was considered in the allometric procedure, AOD increased proportionally more with LBM in boys ($b = 1.03$) than girls ($b = 0.78$). This is likely explained by the closer relationships obtained between age, LBM and AOD in boys. Taken together, these results show that age and LBM both play a major role in explaining sex-related differences in the non-oxidative energy production during high-intensity exercise from the age of 14 years.

From a physiological perspective, sex-related changes in AOD from the age of 14 years could be attributed to hormonal factors and changes in skeletal muscle morphology due to growth and specifically maturation. More explicitly, the greater increase in AOD in boys could be ascribed to their higher production of androgen hormones (e.g., testosterone) at the time of puberty (Korth-Schutz et al. 1976; Fahey et al. 1979). This could increase more favorably muscle mass and the specific area of type II fibres and thereby the activity of non-oxidative metabolism. This hypothesis is supported by some earlier studies showing significant correlations between salivary or blood testosterone concentration, type II fibre area (Mero 1988) and peak lactate concentration in boys (Mero 1988; Falgairette et al. 1991). Oertel (1988) also showed that at least from the age of 15 years, the type II fibre area/type I fibre area ratio in the vastus lateralis and deltoid muscles increases more in boys than girls. In addition, although there is only one study that has compared the muscle enzyme activity during growth and maturation between girls and boys, it is likely that the activity of enolase (i.e., glycolytic enzyme) in the vastus lateralis is greater in boys than girls at 13-15 years of age (Haralambie 1982). This sex-related difference in enzyme activity is consistent with the data reported by Cumming et al. (1985) showing a higher accumulation of serum lactate after maximal exercise in boys compared to girls from the age of 15 years. The results of the present study confirm these data since there was a higher increase in blood lactate concentration and a greater decrease in blood pH and bicarbonate concentration after the 60-s all-out test in boys compared to girls from the age of 16 years. However, sex-related differences were only significant for the maximal blood lactate concentration.

The results of the present study also show that AOD significantly accounted for the mean power output produced during the 60-s all-out test both in girls and boys. This indicates that non-oxidative metabolism could be a major determinant of performance during high-intensity exercise during growth. These results are similar to those of Leclair et al. (2011) which showed a significant positive correlation between AOD expressed in ratio with BM and time to exhaustion during cycle exercise at 100% of maximal aerobic power in 9-11-year-old boys. However, the coefficient of determination was lower in girls ($r^2 = 0.41$) than boys ($r^2 = 0.89$) indicating that AOD is less important in girls in the explanation of the power produced during high-intensity exercise. This may be ascribed to the fact that LBM, which is the main discriminatory factor for AOD and MPO, varied much less in girls than boys (+19% vs. +81%, respectively) and the lower range in LBM values in girls reduced the coefficient of determination (Chen and Popovich 2002). Indirectly, this finding supports the assertion that LBM has a strong influence on AOD and MPO during high-intensity exercise, but this effect is more moderate in girls than boys. Finally, the slopes of relationships between AOD and MPO were not significantly different between girls and boys, suggesting no difference in "anaerobic delta efficiency" between both sexes. However, this finding remains to be confirmed due to the high variance of AOD in girls.

Strengths and limitations

This study presents cross-sectional data and would have been enhanced with measures of maturity status. However, it has been demonstrated that once age and LBM have been controlled for in multiplicative allometric analyses, maturity status does not make an additional, significant contribution to explaining the development of either peak aerobic or peak anaerobic power of 11-18-year-olds (Armstrong and Welsman 2020a, b). The estimation of LBM from BM and skinfold thicknesses rather than its direct measurement using more sophisticated technology can also be criticised, but this methodology is well-established in paediatric exercise physiology (Rowland et al. 1997; Janz et al. 1998; Armstrong and Welsman 2020a, b). Moreover, direct measures of the body fat of children and adolescents have recently been showed to vary widely across laboratory techniques (Ferri-Morales et al. 2018). Finally, we can wonder about the generalization of the present findings to the whole of the pediatric population since rowing is a specific activity involving a larger muscle mass during exercise when compared with cycling or running, for instance (Gastin 2001; Maciejewski et al. 2013).

A unique strength of the present study lies in the adoption for the first time of allometric modelling to analyse youth AOD. This approach has provided new insights into the influence of the contribution of concurrent changes in age and LBM on AOD in childhood and adolescence.

CONCLUSION

The results of the present study show for the first time that energy production derived from non-oxidative metabolism, quantified by AOD during high-intensity exercise, increases with age with boys differing from girls from the age of about 14 years, due to their greater gain in LBM. Boys exhibited significantly higher values of AOD than girls from the age of 14 years but multiplicative allometric modelling showed that when age is considered concurrently with LBM, the sex difference in AOD is reduced during childhood and adolescence. Finally, AOD was found to be a key determinant of performance during high-intensity exercise during childhood and adolescence, particularly in boys owing to their greater LBM gain at the time of puberty.

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Table 1. Participants' physical and fitness characteristics ($n = 74$).

	Group 1 (n=11) 10 – 11.9 yr		**Group 2 (n=17) 12 – 13.9 yr**		**Group 3 (n=27) 14 – 15.9 yr**		**Group 4 (n=19) 16 – 17.9 yr**	
	Girls (n=6)	*Boys (n=5)*	*Girls (n=6)*	*Boys (n=11)*	*Girls (n=15)*	*Boys (n=12)*	*Girls (n=8)*	*Boys (n=11)*
Age (yr)	11.0±0.7	11.5±0.3	12.6±0.7	13.2±0.3	14.8±0.4	14.9±0.6	16.0±0.8	16.9±0.5
Height (m)	1.55±0.05	1.51±0.13	1.63±0.08	1.64±0.08	1.66±0.04	1.79±0.07 **	1.65±0.05	1.78±0.07 **
BM (kg)	48.6±4.8	41.1±8.8	58.8±11.7	53.6±8.7	58.4±6.2	65.6±9.4	56.7±4.5	70.0±5.7 **
Body fat (%)	24.9±6.1	15.7±1.7 **	25.2±5.0	12.9±5.6 ***	21.8±3.5	6.5±1.9 ***	23.1±1.8	10.4±2.0 ***
LBM (kg)	36.3±2.7	34.5±6.9	43.6±7.0	46.7±8.6	45.5±4.5	61.3±8.8 ***	43.5±3.7	62.6±4.9 ***
$\dot{V}O_{2max}$ ($L \cdot min^{-1}$)	1.99±0.2	2.30±0.5	2.32±0.2	2.90±0.7	2.63±0.3	4.14±0.5 ***	2.89±0.3	4.53±0.3 ***

Values are presented as mean ± SD. BM: body mass; LBM: lean body mass; $\dot{V}O_{2max}$: maximal oxygen uptake. **, and ***: significantly different from girls within each age group at $p < 0.01$ and $p < 0.001$, respectively.

Table 2. Mean power output and post-exercise extreme blood responses obtained after a 60-s all-out test in girls (n = 35) and boys (n = 39).

	Group 1 (n=11) 10 – 11.9 yr		**Group 2 (n=17) 12 – 13.9 yr**		**Group 3 (n=27) 14 – 15.9 yr**		**Group 4 (n=19) 16 – 17.9 yr**	
	Girls (n=6)	*Boys (n=5)*	*Girls (n=6)*	*Boys (n=11)*	*Girls (n=15)*	*Boys (n=12)*	*Girls (n=8)*	*Boys (n=11)*
MPO (W)	153±16	178±45	219±40	276±71 †	261±33 ††	440±76 †††, ***	283±43 †††	520±55 †††, ***
$[La]_{max}$ ($mmol \cdot L^{-1}$)	8.2±1.0	9.3±1.4	10.5±0.7	11.4±0.8	12.3±2.0 †††	14.1±1.5 †††	12.3±1.8 †††	16.4±1.9 †††, **
pH_{min}	7.27±0.02	7.27±0.03	7.21±0.05	7.22±0.02	7.20±0.05	7.17±0.05	7.19±0.04	7.12±0.05
$[HCO_3^-]_{min}$ ($mmol \cdot L^{-1}$)	15.9±1.0	14.3±1.6	12.4±1.4	11.0±2.3	12.1±2.2	9.6±2.1	11.4±1.7	9.7±1.5

MPO: mean power output; $[La]_{max}$: maximal blood lactate concentration; pH_{min}: minimal blood pH; $[HCO_3^-]_{min}$: minimal blood bicarbonate ions concentration. Values are presented as mean ± SD. †, ††, †††: significantly different from the group 1 within each sex category at $p < 0.05$, $p < 0.01$, and $p < 0.001$. *, **, and ***: significantly different from girls within each age group at $p < 0.05$, $p < 0.01$, and $p < 0.001$ respectively.

FIGURE LEGENDS

Figure 1. AOD expressed in absolute values (Panel A), in ratio with BM (Panel B), and with allometric exponents (Panel C) by age group and sex (girls in white bars and boys in black bars).

Figure 2. Relationships between AOD (L O_2 Eq.) and MPO (W) in girls (white circles and dash line) and boys (black circles and full line). The 95% confidence intervals are shown in gray. The regressions obtained between AOD and MPO were adjusted on x-axis (AOD) since estimation error could be greater on AOD than MPO.

Figure 1

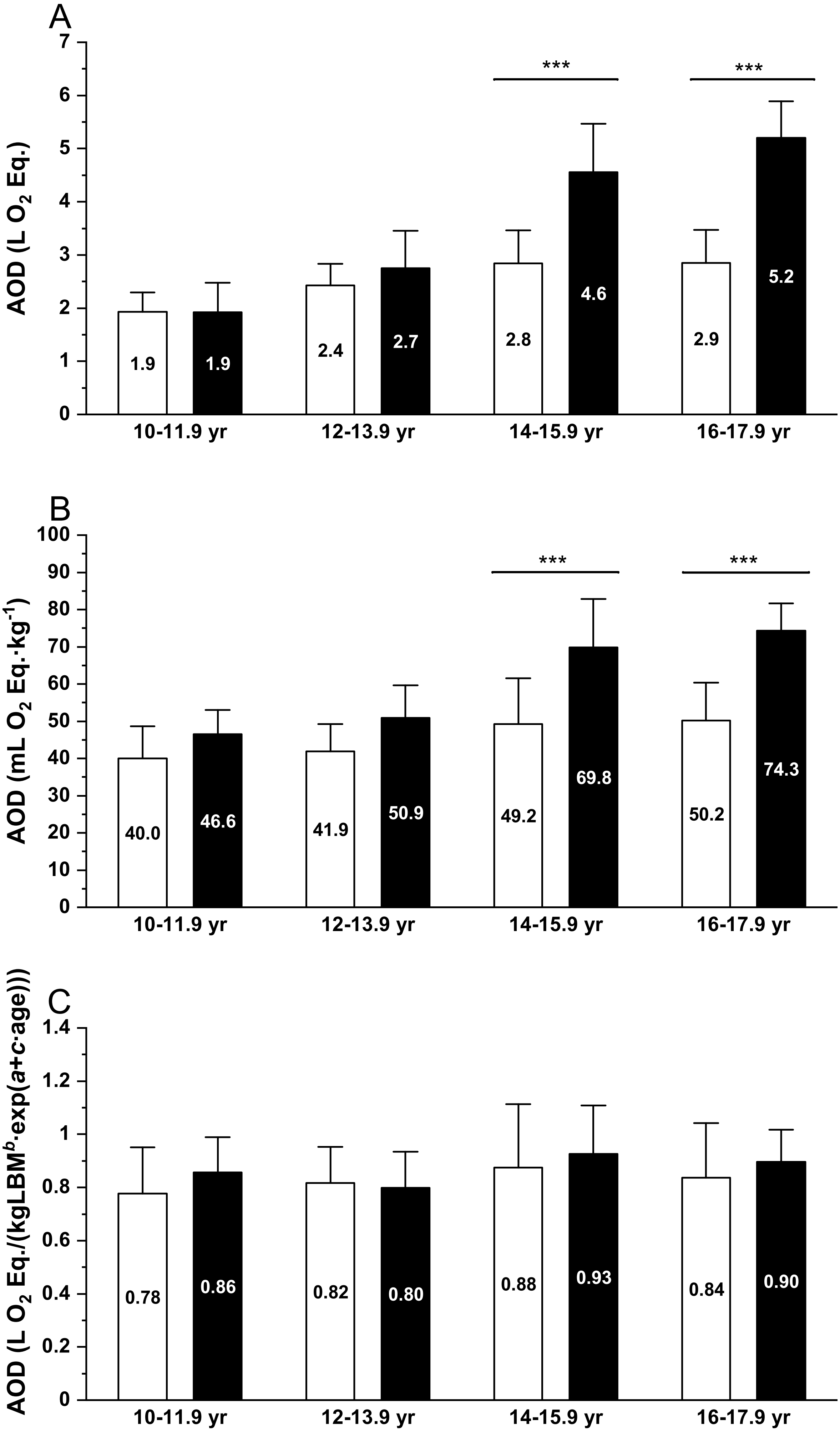
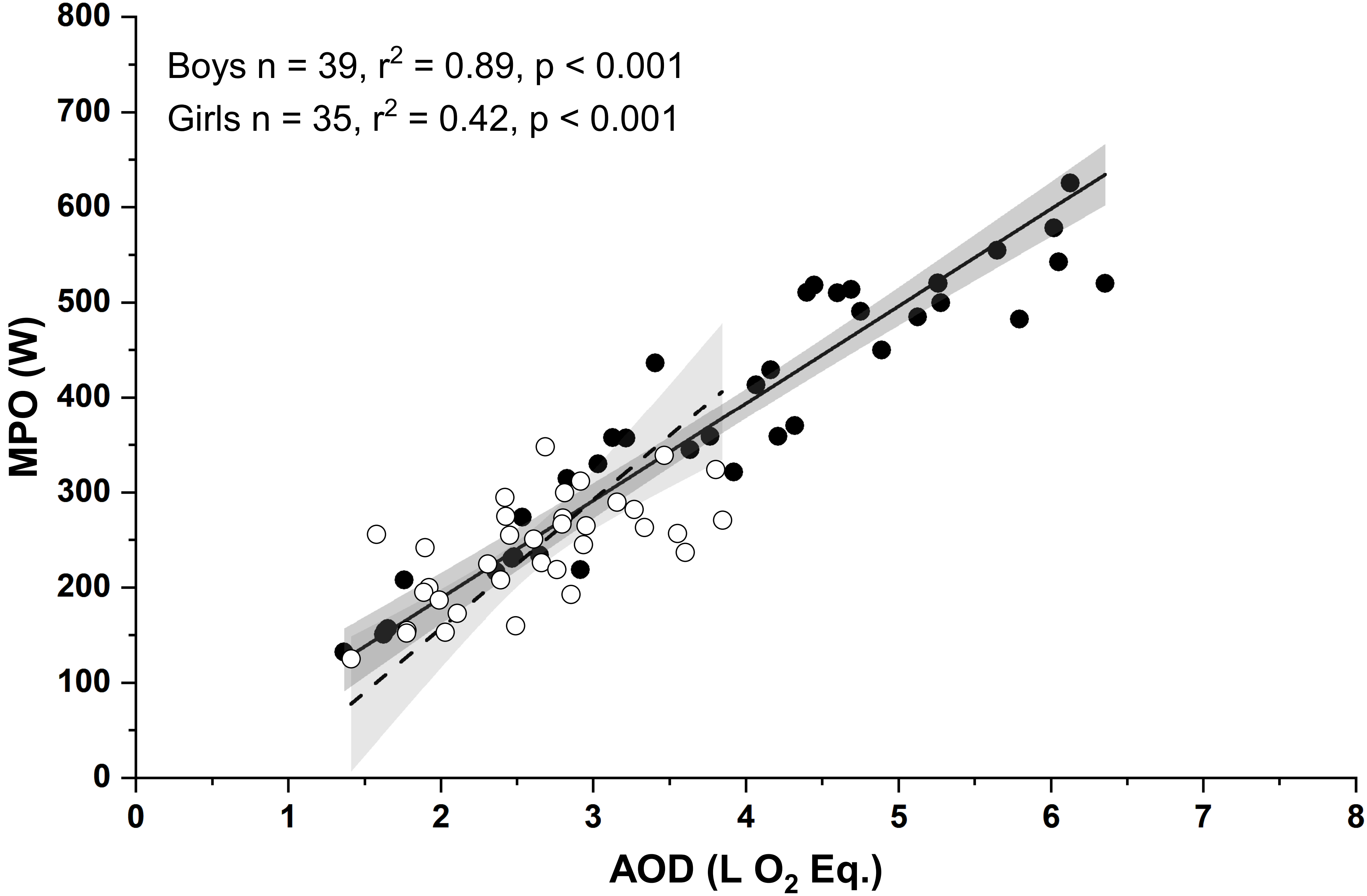

A
AOD (L O_2 Eq.)
***
***
1.9
1.9
2.4
2.7
2.8
4.6
2.9
5.2
10-11.9 yr
12-13.9 yr
14-15.9 yr
16-17.9 yr
B
AOD (mL O_2 Eq.·kg^{-1})
***
***
40.0
46.6
41.9
50.9
49.2
69.8
50.2
74.3
10-11.9 yr
12-13.9 yr
14-15.9 yr
16-17.9 yr
C
AOD (L O_2 Eq./(kgLBM^b·exp(a+c·age)))
0.78
0.86
0.82
0.80
0.88
0.93
0.84
0.90
10-11.9 yr
12-13.9 yr
14-15.9 yr
16-17.9 yr

Figure 2



Boys n = 39, r2 = 0.89, p < 0.001
Girls n = 35, r2 = 0.42, p < 0.001
MPO (W)
AOD (L O2 Eq.)
0
100
200
300
400
500
600
700
800
0
1
2
3
4
5
6
7
8