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1 Original article

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3 **Sex-related differences in accumulated O<sub>2</sub> deficit incurred by high-intensity**  
4 **rowing exercise during childhood and adolescence**

5

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36

37 **DECLARATIONS**

38 **Author contribution statement**

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

47

48 **Ethics approval**

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

53

54 **Consent to participate**

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

57

58 **Consent for publication**

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

61

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67

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69 The authors have no funding sources to declare.

70

71 **Conflict of interest**

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

74

75 **ABSTRACT**

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

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

83 **Results:** AOD significantly increased with age in both sexes ( $p < 0.001$ ) with boys exhibiting  
84 significantly higher AOD than girls from the age of 14 years (10-11.9 yr: 1.9 vs 1.9 L, 12-  
85 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  
86 respectively,  $p < 0.001$ ). However, a sex difference was no longer significant when AOD was  
87 analysed using an allometric model including age and LBM ( $p = 0.885$ ). Finally, significant  
88 correlations were found between AOD and MPO in boys and girls but with lower evidence in  
89 girls ( $r^2 = 0.41$  vs.  $0.89$ ).

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

94

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

97

98 **ABBREVIATIONS**

99	ANCOVA	Analysis of covariance
100	ANOVA	Analysis of variance
101	AOD	Accumulated oxygen deficit
102	BM	Body mass
103	$[\text{HCO}_3^-]_{\text{min}}$	Minimal blood bicarbonate concentration
104	$[\text{La}]_{\text{max}}$	Maximal blood lactate concentration
105	LBM	Lean body mass
106	MPO	Mean power output
107	$\text{pH}_{\text{min}}$	Minimal blood pH
108	$\dot{V}\text{O}_{2\text{max}}$	Maximal oxygen uptake
109	$\dot{V}\text{O}_{2\text{rest}}$	Oxygen uptake at rest

## 110 INTRODUCTION

111 It is well-established that the development of body composition during childhood and  
112 adolescence is sex-specific (Baxter-Jones et al. 2003; Wells 2007). Indeed, post-pubertal  
113 boys acquire a greater lean body mass (LBM) and less fat mass than post-pubertal girls  
114 during late adolescence (Baxter-Jones et al. 2003; Wells 2007). As fat is metabolically inert  
115 (Goran et al. 2000), this sexual dimorphism during puberty strongly influences performance  
116 during high-intensity exercise. For instance, peak power output (in W) increases significantly  
117 in both sexes from childhood into adolescence (Doré et al. 2001; Martin et al. 2003;  
118 Armstrong and Welsman 2019a) but from 13-14 years of age boys develop higher peak  
119 power output than girls (Blimkie et al. 1988; Armstrong et al. 1997; Martin et al. 2004; Doré  
120 et al. 2005; Mikulic and Markovic 2011; Armstrong and Welsman 2019a). Several authors  
121 have suggested that these differences in performance between girls and boys from the age of  
122 13-14 years are influenced by non-oxidative energy output in addition to differences in body  
123 composition (Malina et al. 2004; Doré et al. 2005). However, while it is well-established that  
124 the contribution of non-oxidative metabolism during high-intensity exercise is greater in post-  
125 than pre-pubertal boys (Birat et al. 2018; Ratel et al. 2002b, a), no previous study has  
126 evaluated non-oxidative energy production during childhood and adolescence with respect to  
127 sex, or established any direct relationship between non-oxidative metabolism and  
128 performance during high-intensity exercise from childhood into adolescence.

129 The activity of non-oxidative metabolism can be assessed using several different  
130 methods such as muscle biopsy (Eriksson et al. 1971) or phosphorus<sup>31</sup> magnetic resonance  
131 spectroscopy (Tonson et al. 2010). However, for ethical or technological reasons, these  
132 techniques have not been used to evaluate the importance of non-oxidative metabolism in the  
133 relative development of the performance of girls and boys. Alternatively, blood lactate assays  
134 have been used to explore non-oxidative (glycolytic) metabolism during childhood and

135 adolescence, with only one study reporting a lower blood lactate response following maximal  
136 exercise in girls compared to boys, from the age of 16 years (Cumming et al. 1985).  
137 However, blood lactate concentration must be interpreted cautiously as lactate sampled in  
138 blood cannot be assumed to reflect a consistent or direct relationship with muscle lactate  
139 production. The physiological relevance of this blood marker to assess non-oxidative energy  
140 turnover during high-intensity whole-body exercise is, therefore, highly debatable (Ferguson  
141 et al. 2018).

142         Among other methods, the measurement of accumulated O<sub>2</sub> deficit (AOD) has been  
143 found to be a valid technique in adults (Medbø et al. 1988) and children (Naughton and  
144 Carlson 1995) to assess non-oxidative energy production during high-intensity, whole-body  
145 exercise. However, use of this method with children and adolescents has seldom been  
146 reported. To our knowledge, three studies have reported lower AOD, whether expressed in  
147 absolute terms or in ratio with body mass (BM) in 9-12-year-old boys than male adolescents  
148 or young men (Hebestreit et al. 1998; Leclair et al. 2011; Diry et al. 2020), thereby  
149 suggesting an age effect on non-oxidative energy metabolism. Furthermore, while a sex-  
150 related difference in AOD of ~15-25% (relative to body dimensions) has been observed in  
151 adults (Medbø and Burgers 1990; Weyand et al. 1993; Ramsbottom et al. 1997; Weber and  
152 Schneider 2000), no previous study has analysed changes in AOD during childhood and  
153 adolescence with respect to sex. No differences in AOD or AOD relative to BM have been  
154 reported during high-intensity exercise between 9-11-year-old non-athletic girls and boys  
155 (Carlson and Naughton 1993; Naughton and Carlson 1995; Berthoin et al. 2003). In addition,  
156 the only study to have analysed the sex-related difference in AOD in 14-15-year-olds showed  
157 that trained girls (n = 8) had significantly lower absolute AOD and AOD relative to BM than  
158 trained boys (n = 8) when exercising on an inclined treadmill at two constant exercise  
159 intensities (120 and 130% of maximal aerobic power) (Naughton et al. 1997). These

160 differences were also found in performance, as running speed was significantly higher in  
161 boys than girls at both exercise intensities (Naughton et al. 1997).

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

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

185 power, peak power output, and mean power output is concurrent changes in age and LBM, as  
186 reflected by the combination of BM and skinfold thicknesses (Armstrong and Welsman  
187 2019a, b).

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

197

## 198 **MATERIALS AND METHODS**

### 199 **Subjects**

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

## 210 **Experimental design**

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

223

## 224 **Experimental measurements**

### 225 **Session 1**

#### 226 *Anthropometric characteristics and body composition*

227           BM (in kg) was measured using a digital weight scale with a precision of  $\pm 0.01$  kg  
228 (Seca 899, Seca, Germany). Standing height (in m) was assessed using a stadiometer with a  
229 precision of  $\pm 1$  mm (Seca 213, Seca, Germany). Skinfold thicknesses were measured at the  
230 triceps and subscapular sites using a Harpenden calliper (British Indicators Ltd, St Albans,  
231 UK) and the mean value from three reproducible measurements was calculated. The  
232 measurements were taken by the same experienced investigator on the right side of the body  
233 to reduce variability in the results for girls and boys. Body fat percentage and LBM (in kg)  
234 were determined using the equations developed by Slaughter et al. (1988). These equations

235 are specific to sex, ethnicity, and age, and are recommended for assessing body fat and LBM  
236 in children 8-18 years of age.

237

### 238 *Maximal oxygen uptake test*

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

246 Oxygen uptake, carbon dioxide output and ventilation were continuously monitored  
247 using a breath-by-breath analyser (Quark CPET, Cosmed, Italy). Heart rate was continuously  
248 recorded with a heart rate monitor (HRM-Dual, Garmin, Kansas, USA).  $\dot{V}O_{2\max}$  was  
249 considered to be reached during the last step when at least two of the following criteria were  
250 met: (i)  $\dot{V}O_2$  levelling-off, (ii) maximal respiratory exchange ratio  $\geq 1.1$ , (iii) maximal heart  
251 rate  $\geq 95\%$  of the age-predicted maximal heart rate ( $208.609 - 0.716 \cdot \text{age}$ ) (Shargal et al.  
252 2015) and (iv) blood lactate concentration higher than 8 mmol·L<sup>-1</sup>.

253

## 254 **Session 2**

### 255 *60-s all-out test*

256 After a standardised 15-min warm-up at about 130-140 beats·min<sup>-1</sup> and two short  
257 sprints (10-s) in the last five minutes, all participants performed a 60-s all-out test. This test  
258 was followed by a 10-min sitting recovery. Cardio-respiratory parameters were continuously  
259 measured using a breath-by-breath analyzer (Quark CPET, Cosmed, Italy). Capillary

260 arterialised blood samples (80  $\mu$ L) were drawn from the earlobe and collected after warm-up  
261 and at 1-, 3-, 5-, and 8-min post-exercise to measure the time course of pH, bicarbonate  
262 ( $[\text{HCO}_3^-]$  in  $\text{mmol}\cdot\text{L}^{-1}$ ) and lactate ([La]). Whole blood [La] was determined enzymatically  
263 using the same lactate analyser as in the first session while blood pH and  $[\text{HCO}_3^-]$  were  
264 measured by direct potentiometry using an i-STAT $\text{\textcircled{R}}$  handheld analyser (Abbott Point of  
265 Care, Princeton, USA) immediately after collection. The maximal lactate concentration  
266 ( $[\text{La}]_{\text{max}}$ ), the minimal pH value ( $\text{pH}_{\text{min}}$ ) and the minimal bicarbonate ions concentration  
267 ( $[\text{HCO}_3^-]_{\text{min}}$ ) were identified. Mean power output (MPO in W) was calculated over the entire  
268 test and individual AOD (in L  $\text{O}_2$  Eq.) was determined according to the procedure described  
269 below.

270

## 271 **Measurements and calculations**

### 272 *Accumulated oxygen deficit*

273 AOD was determined by subtracting accumulated  $\text{O}_2$  uptake (the measured  $\text{O}_2$  uptake  
274 integrated over time) from accumulated  $\text{O}_2$  demand (the estimated  $\text{O}_2$  demand integrated over  
275 time). In accordance with Green and Dawson (1996), oxygen demand was extrapolated using  
276 the equation of the  $\dot{V}\text{O}_2$ -power output linear regression obtained during the incremental test  
277 and considering the individual value of  $\dot{V}\text{O}_{2\text{rest}}$  (i.e.,  $\dot{V}\text{O}_2$  measured during a period of three  
278 minutes before the test). The squared Bravais-Pearson correlation coefficients of linear  
279 relationships between  $\dot{V}\text{O}_2$  and power output ranged between 0.92 and 0.99 (mean  $\pm$  SD: 0.98  
280  $\pm$  0.02). Because the present study concerned all-out exercise,  $\text{O}_2$  demand was calculated  
281 from instantaneous power output (recorded stroke by stroke) rather than mean power output  
282 sustained during exercise (i.e., MPO) as initially proposed by Medbø et al. (1988).

283

284

285 *Allometric modelling procedure*

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

290

$$291 \quad \text{AOD} = \text{LBM}^b \cdot \exp(a + c \cdot \text{age}) \cdot \varepsilon \quad (\text{Eq. 1})$$

292

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

297

$$298 \quad \log(\text{AOD}) = b \cdot \log(\text{LBM}) + a + c \cdot \text{age} + \log \varepsilon \quad (\text{Eq. 2})$$

299

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

302

303 **Statistical analysis**

304 Statistical procedures were performed using Statistica 8.0 software (Statsoft, Inc.,  
305 USA). Descriptive statistics were expressed as mean  $\pm$  standard deviation (SD) by age group  
306 (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,  
307 as proposed by Doré et al. (2005). Data were screened for normality of distribution and  
308 homogeneity of variances using a Shapiro-Wilk test and the Levene's test, respectively. Two-  
309 way ANOVA was used to examine the effects of sex and age group on AOD and for

310 comparative purposes AOD in ratio with BM. When ANOVA revealed a main or interaction  
311 significant effect, an HSD Tukey's *post-hoc* test was applied to test the discrimination  
312 between means. The effect size and statistical power have also been reported. The effect size  
313 was assessed using the partial eta-squared ( $\eta^2$ ) and ranked as follows:  $\sim 0.01$  = small effect,  
314  $\sim 0.06$  = moderate effect,  $\geq 0.14$  = large effect (Cohen 1969). Linear regression models  
315 between age, LBM, AOD, and MPO were fitted by the least-squares method by considering  
316 boys and girls separately, and the squared Bravais-Pearson determination coefficients ( $r^2$ ) of  
317 these linear regression models were calculated. The linear regressions between age, LBM and  
318 AOD were established in order to check the effects of age and LBM on AOD and then justify  
319 the use of age and LBM as scaling factors through the multiplicative allometric model. The  
320 slopes of relationships between AOD and MPO were compared between girls and boys using  
321 an analysis of covariance (ANCOVA). This procedure was done with an adjustment on x-  
322 axis (AOD) since estimation error could be greater on AOD than MPO (Brace 1977). The  
323 statistical significance level was set at 5% ( $p < 0.05$ ).

324

## 325 **RESULTS**

### 326 **Participants' physical and fitness characteristics**

327 Participants' characteristics are described by age group and sex in Table 1. Statistical  
328 analysis revealed no significant sex x age group interaction effect for age [ $F_{(3, 66)} = 1.29$ ,  $p =$   
329  $0.28$ ,  $\eta^2 = 0.06$ , power = 0.33]. However, there were significant sex x age group interaction  
330 effects for height [ $F_{(3, 66)} = 4.83$ ,  $p < 0.01$ ,  $\eta^2 = 0.18$ , power = 0.89], BM [ $F_{(3, 66)} = 6.55$ ,  $p <$   
331  $0.001$ ,  $\eta^2 = 0.23$ , power = 0.96], LBM [ $F_{(3, 66)} = 9.29$ ,  $p < 0.001$ ,  $\eta^2 = 0.30$ , power = 0.99],  
332 and  $\dot{V}O_{2\max}$  [ $F_{(3, 65)} = 8.69$ ,  $p < 0.001$ ,  $\eta^2 = 0.29$ , power = 0.99]. No sex-related significant  
333 difference was observed for height, BM, LBM and  $\dot{V}O_{2\max}$  before the age of 14 years.  
334 However, between 14.0 and 17.9 years, boys exhibited significantly higher values for height,

335 BM, LBM and  $\dot{V}O_{2\max}$ . Statistical analysis also revealed a significant sex effect for body fat  
336 percentage [ $F_{(1, 66)} = 175.5$ ,  $p < 0.001$ ,  $\eta^2 = 0.73$ , power = 1.00]. Girls displayed significantly  
337 higher values of body fat percentage than boys between 10.0 and 17.9 years ( $p < 0.01$ , at  
338 least).

339 - Please insert Table 1 near here -

340

### 341 **Determination coefficients and allometric exponents**

342 Age was positively correlated to LBM in boys ( $r^2 = 0.62$ ,  $p < 0.001$ ) and girls ( $r^2 =$   
343  $0.13$ ,  $p < 0.05$ ). Age was also positively correlated to AOD in boys ( $r^2 = 0.72$ ,  $p < 0.001$ ) and  
344 girls ( $r^2 = 0.23$ ,  $p < 0.01$ ). In addition, LBM was positively associated with AOD in boys ( $r^2 =$   
345  $0.75$ ,  $p < 0.001$ ) and girls ( $r^2 = 0.22$ ,  $p < 0.01$ ), and with MPO in boys ( $r^2 = 0.86$ ,  $p < 0.001$ )  
346 and girls ( $r^2 = 0.47$ ,  $p < 0.001$ ).

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

350

### 351 **Accumulated Oxygen Deficit (AOD)**

352 AOD values are displayed in absolute terms (L O<sub>2</sub> Eq.) and in ratio with BM (mL O<sub>2</sub>  
353 Eq. $\cdot$ kg<sup>-1</sup>BM) as well as with allometric exponents for LBM and age [L O<sub>2</sub> Eq. / (kg LBM <sup>$b$</sup>  $\cdot$   
354  $\exp(a + c \cdot \text{age})$ )] by age group and sex in Figure 1. Regardless of sex, AOD increased with  
355 age whether in absolute [ $F_{(3, 66)} = 31.49$ ,  $p < 0.001$ ,  $\eta^2 = 0.59$ , power = 1.00] or in ratio with  
356 BM [ $F_{(3, 66)} = 13.44$ ,  $p < 0.001$ ,  $\eta^2 = 0.38$ , power = 0.99]. Two-way ANOVA also revealed a  
357 significant sex x age group interaction effect for absolute AOD [ $F_{(3, 66)} = 10.84$ ,  $p < 0.001$ ,  $\eta^2 =$   
358  $0.33$ , power = 0.99] and AOD expressed in ratio with BM [ $F_{(3, 66)} = 2.79$ ,  $p = 0.05$ ,  $\eta^2 =$   
359  $0.11$ , power = 0.64]. *Post-hoc* tests showed significantly higher values for absolute AOD and

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

364

365 - Please insert Figure 1 near here -

366

### 367 **MPO and post-exercise blood responses**

368 Mean power output (MPO) and post-exercise extreme blood responses ( $[La]_{max},$   
369  $pH_{min}, [HCO_3^-]_{min}$ ) are described by age group and sex in Table 2. Two-way ANOVA showed  
370 significant sex x age group interaction effects for MPO [ $F_{(3, 66)} = 13.4, p < 0.001, \eta^2 = 0.38,$   
371 power = 0.99] and  $[La]_{max}$  [ $F_{(3, 66)} = 3.78, p < 0.05, \eta^2 = 0.15, \text{power} = 0.79$ ] but not for blood  
372  $pH_{min}$  [ $F_{(3, 64)} = 2.0, p = 0.11, \eta^2 = 0.09, \text{power} = 0.51$ ] and  $[HCO_3^-]_{min}$  [ $F_{(3, 61)} = 0.34, p =$   
373  $0.799, \eta^2 = 0.02, \text{power} = 0.11$ ]. MPO and  $[La]_{max}$  significantly increased with increasing age  
374 and values were significantly higher between 16.0 and 17.9 years for  $[La]_{max}$  ( $p < 0.001$ ) and  
375 between 14.0 and 17.9 years for MPO ( $p < 0.001$ ).

376

377 - Please insert Table 2 near here -

378

### 379 **Relationships between AOD and MPO**

380 The relationships between AOD (L O<sub>2</sub> Eq.) and MPO (W) in boys and girls are  
381 displayed in Figure 2. Significant positive relationships were observed between AOD and  
382 MPO in boys ( $r^2 = 0.89, p < 0.001$ ) and girls ( $r^2 = 0.41, p < 0.001$ ). The slopes of  
383 relationships between AOD and MPO were not significantly different between both sexes [ $F$   
384  $(1, 70) = 2.30, p = 0.13, \eta^2 = 0.03, \text{power} = 0.32$ ].

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- Please insert Figure 2 near here -

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## 388 **DISCUSSION**

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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

410 studies showed a difference in AOD between prepubertal boys and young men; however,  
411 these studies were not designed to test the effect of age and employed small sample numbers  
412 with a lack of continuity from childhood into adolescence (Hebestreit et al. 1998; Leclair et  
413 al. 2011). The results also show sex-related differences in AOD to only be present from the  
414 age of 14 years. These results are consistent with previously published studies of AOD in  
415 ratio with BM, which showed with small samples no sex differences in AOD between 9-11-  
416 year-olds (Carlson and Naughton 1993; Naughton and Carlson 1995; Berthoin et al. 2003)  
417 but significantly higher AOD values in boys than girls at 14-15 years (Naughton et al. 1997).

418

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

430

431         From a physiological perspective, sex-related changes in AOD from the age of 14  
432 years could be attributed to hormonal factors and changes in skeletal muscle morphology due  
433 to growth and specifically maturation. More explicitly, the greater increase in AOD in boys  
434 could be ascribed to their higher production of androgen hormones (e.g., testosterone) at the

435 time of puberty (Korth-Schutz et al. 1976; Fahey et al. 1979). This could increase more  
436 favorably muscle mass and the specific area of type II fibres and thereby the activity of non-  
437 oxidative metabolism. This hypothesis is supported by some earlier studies showing  
438 significant correlations between salivary or blood testosterone concentration, type II fibre  
439 area (Mero 1988) and peak lactate concentration in boys (Mero 1988; Falgairette et al. 1991).  
440 Oertel (1988) also showed that at least from the age of 15 years, the type II fibre area/type I  
441 fibre area ratio in the vastus lateralis and deltoid muscles increases more in boys than girls. In  
442 addition, although there is only one study that has compared the muscle enzyme activity  
443 during growth and maturation between girls and boys, it is likely that the activity of enolase  
444 (i.e., glycolytic enzyme) in the vastus lateralis is greater in boys than girls at 13-15 years of  
445 age (Haralambie 1982). This sex-related difference in enzyme activity is consistent with the  
446 data reported by Cumming et al. (1985) showing a higher accumulation of serum lactate after  
447 maximal exercise in boys compared to girls from the age of 15 years. The results of the  
448 present study confirm these data since there was a higher increase in blood lactate  
449 concentration and a greater decrease in blood pH and bicarbonate concentration after the 60-s  
450 all-out test in boys compared to girls from the age of 16 years. However, sex-related  
451 differences were only significant for the maximal blood lactate concentration.

452

453         The results of the present study also show that AOD significantly accounted for the  
454 mean power output produced during the 60-s all-out test both in girls and boys. This indicates  
455 that non-oxidative metabolism could be a major determinant of performance during high-  
456 intensity exercise during growth. These results are similar to those of Leclair et al. (2011)  
457 which showed a significant positive correlation between AOD expressed in ratio with BM  
458 and time to exhaustion during cycle exercise at 100% of maximal aerobic power in 9-11-  
459 year-old boys. However, the coefficient of determination was lower in girls ( $r^2 = 0.41$ ) than

460 boys ( $r^2 = 0.89$ ) indicating that AOD is less important in girls in the explanation of the power  
461 produced during high-intensity exercise. This may be ascribed to the fact that LBM, which is  
462 the main discriminatory factor for AOD and MPO, varied much less in girls than boys (+19%  
463 vs. +81%, respectively) and the lower range in LBM values in girls reduced the coefficient of  
464 determination (Chen and Popovich 2002). Indirectly, this finding supports the assertion that  
465 LBM has a strong influence on AOD and MPO during high-intensity exercise, but this effect  
466 is more moderate in girls than boys. Finally, the slopes of relationships between AOD and  
467 MPO were not significantly different between girls and boys, suggesting no difference in  
468 “anaerobic delta efficiency” between both sexes. However, this finding remains to be  
469 confirmed due to the high variance of AOD in girls.

470

#### 471 **Strengths and limitations**

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

484 a larger muscle mass during exercise when compared with cycling or running, for instance  
485 (Gastin 2001; Maciejewski et al. 2013).

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

490

## 491 **CONCLUSION**

492 The results of the present study show for the first time that energy production derived  
493 from non-oxidative metabolism, quantified by AOD during high-intensity exercise, increases  
494 with age with boys differing from girls from the age of about 14 years, due to their greater  
495 gain in LBM. Boys exhibited significantly higher values of AOD than girls from the age of  
496 14 years but multiplicative allometric modelling showed that when age is considered  
497 concurrently with LBM, the sex difference in AOD is reduced during childhood and  
498 adolescence. Finally, AOD was found to be a key determinant of performance during high-  
499 intensity exercise during childhood and adolescence, particularly in boys owing to their  
500 greater LBM gain at the time of puberty.

501

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659

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

	<b>Group 1 (n=11)</b> <b>10 – 11.9 yr</b>		<b>Group 2 (n=17)</b> <b>12 – 13.9 yr</b>		<b>Group 3 (n=27)</b> <b>14 – 15.9 yr</b>		<b>Group 4 (n=19)</b> <b>16 – 17.9 yr</b>	
	<i>Girls</i> (n=6)	<i>Boys</i> (n=5)	<i>Girls</i> (n=6)	<i>Boys</i> (n=11)	<i>Girls</i> (n=15)	<i>Boys</i> (n=12)	<i>Girls</i> (n=8)	<i>Boys</i> (n=11)
<b>Age (yr)</b>	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
<b>Height (m)</b>	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 **
<b>BM (kg)</b>	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 **
<b>Body fat (%)</b>	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 ***
<b>LBM (kg)</b>	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 ***
<b><math>\dot{V}O_{2max}</math> (L·min<sup>-1</sup>)</b>	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).

	<b>Group 1 (n=11)</b> <b>10 – 11.9 yr</b>		<b>Group 2 (n=17)</b> <b>12 – 13.9 yr</b>		<b>Group 3 (n=27)</b> <b>14 – 15.9 yr</b>		<b>Group 4 (n=19)</b> <b>16 – 17.9 yr</b>	
	<i>Girls</i> (n=6)	<i>Boys</i> (n=5)	<i>Girls</i> (n=6)	<i>Boys</i> (n=11)	<i>Girls</i> (n=15)	<i>Boys</i> (n=12)	<i>Girls</i> (n=8)	<i>Boys</i> (n=11)
<b>MPO (W)</b>	153±16	178±45	219±40	276±71 †	261±33 ††	440±76 †††, ***	283±43 †††	520±55 †††, ***
<b>[La]<sub>max</sub> (mmol·L<sup>-1</sup>)</b>	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 †††, **
<b>pH<sub>min</sub></b>	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
<b>[HCO<sub>3</sub><sup>-</sup>]<sub>min</sub> (mmol·L<sup>-1</sup>)</b>	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]<sub>max</sub>: maximal blood lactate concentration; pH<sub>min</sub>: minimal blood pH; [HCO<sub>3</sub><sup>-</sup>]<sub>min</sub>: 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

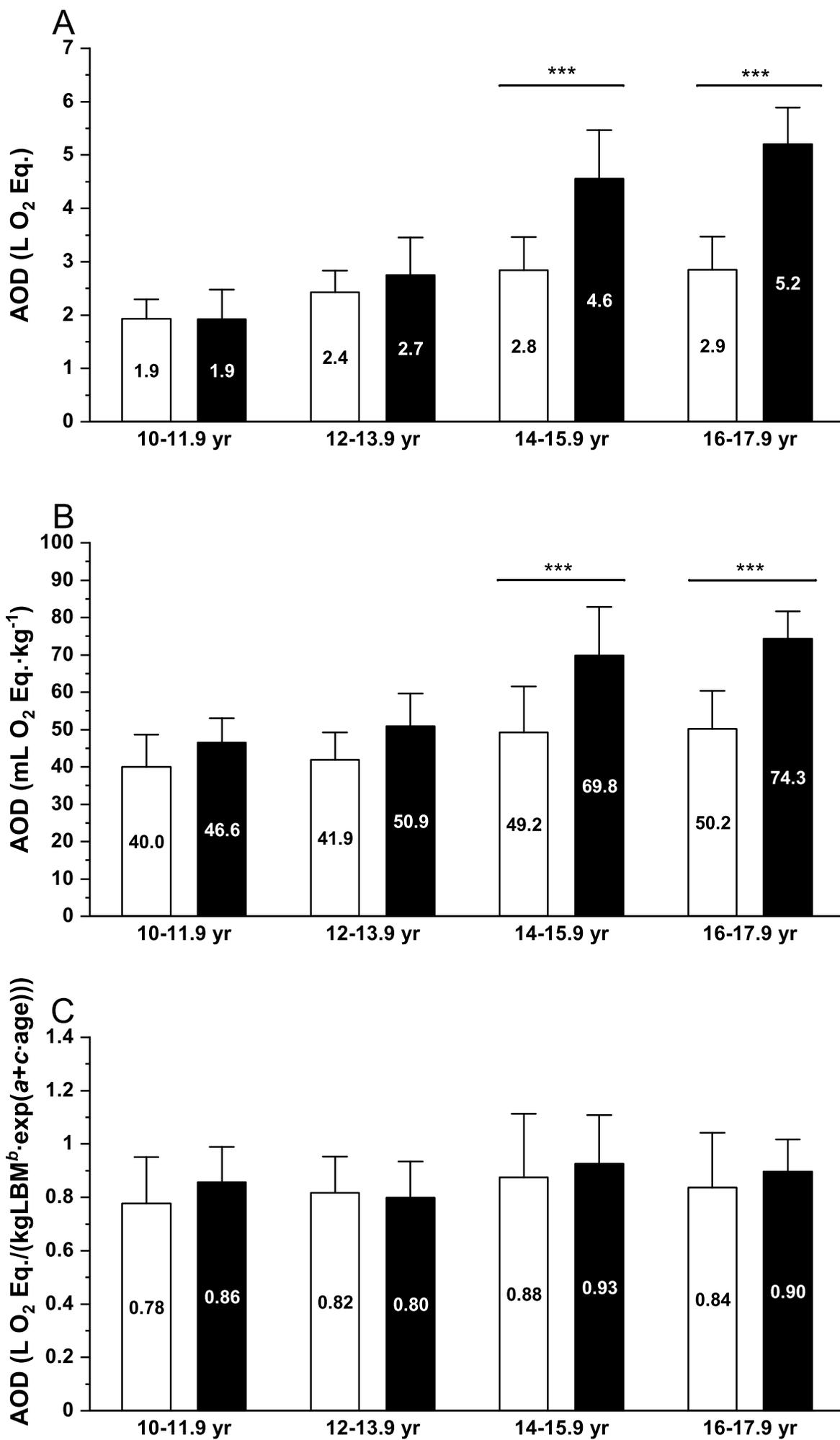


Figure 2

