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Physiological requirements in triathlon

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ABSTRACT

Millet GP, Vleck VE, Bentley DJ. Physiological requirements in triathlon. *J. Hum. Sport Exerc.* Vol. 6, No. 2, pp. 184-204, 2011. This article aims to present the current knowledge on physiological requirements in Olympic distance and Ironman triathlon. Showing the data available from a “traditional point of view” (aerobic power, anaerobic threshold, heart rate, running economy) and from a “contemporary” point of view ($\dot{V}O_2$ kinetics), it emphasises where we are currently and the areas that remain unknown. **Key words:** MAXIMAL AEROBIC POWER, ANAEROBIC THRESHOLD, HEART RATE, RUNNING ECONOMY, VO_2 KINETICS, OLYMPIC DISTANCE, IRONMAN.

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INTRODUCTION

Exercise physiologists working with triathletes have to deal (1) with different exercise modes; (2) inter-individual variations in swim, cycle and run training history that in turn influence athlete's training adaptations and training profiles; (3) different genders and finally (4) different triathlon distances (in this article, we shall focus only on Olympic distance OD vs. Long Distance LD).

'Traditional' viewpoint

Traditionally (Burnley & Jones, 2007; Coyle, 1995; di Prampero, Atchou, Bruckner, Moia, 1986; Joyner & Coyle, 2008), endurance performance is thought to be mainly determined by the following factors: maximal oxygen consumption ($\dot{V}O_{2\max}$); lactate/ventilatory threshold (LT/VT) and economy/efficiency (Figure 1) together with – depending on the distance and the authors – anaerobic capacity (AC) or critical power (CP).

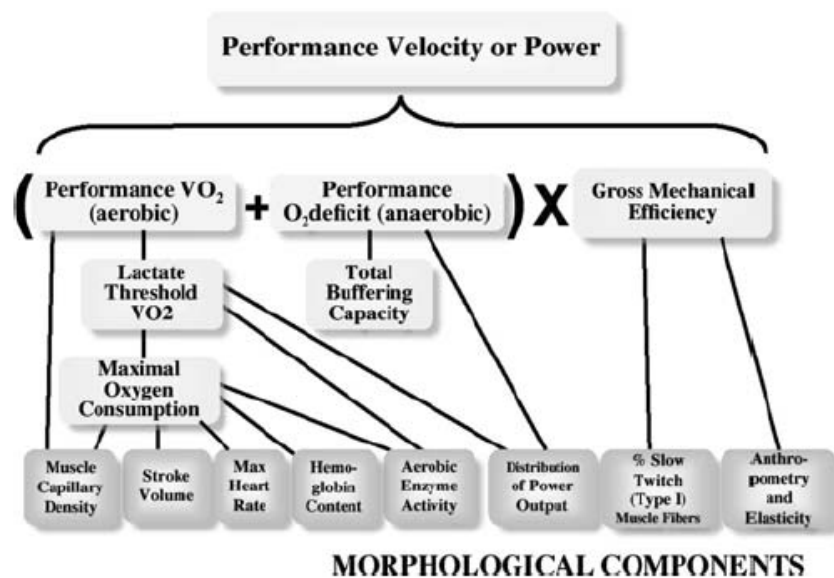


Figure 1. Overall schematic of the multiple 'traditional' physiological factors that interact as determinants of performance velocity or power output (Coyle, 1995).

It is of interest to note that only the two first of these factors ($\dot{V}O_{2\max}$ and LT/VT) have been extensively investigated in triathletes.

"Performance $\dot{V}O_2$ " (*i.e.* how long a given rate of aerobic and anaerobic metabolism can be sustained) is determined by the interaction between $\dot{V}O_{2\max}$ and lactate threshold (LT), whereas efficiency determines how much speed or power (*i.e.* "performance velocity") can be achieved for a given amount of energy consumption (Joyner & Coyle, 2008). However, these physiological variables measured in either cycling and running may adapt indifferently as a consequence of cross training in cycling and running (Loy, Hoffmann, Holland, 1995; Tanaka, 1994; Sleivert & Rowlands, 1996; Pechar, McArdle, Katch, Magel, DeLuca, 1974; Withers, Sherman, Miller, Costill, 1981; Fernhall & Kohrt, 1990; Basset & Boulay, 2000; Hue, Le Gallais, Chollet, Prefaut, 2000; Schneider, Lacroix, Atkinson, Troped, Pollack, 1990; Millet, Dreano, Bentley, 2003; Kreider, 1988): -cross training being defined as 'combined alternative training modes within a sport specific regime'. It is also possible that the results of such physiological tests in cycling and running may be influenced by the athlete's original training background. By comparing physiological variables as maximal oxygen consumption ($\dot{V}O_{2\max}$), anaerobic threshold (AT), heart rate, economy or delta efficiency measured in cycling and running in triathletes, we aimed to identify the effects of exercise mode on, and whether triathletes competing in OD vs LD events differ as regards, physiological profile.

'Contemporary' viewpoint

Recently (Burnley & Jones, 2007), it has been suggested that "these 'traditional' parameters are important because they determine the character of, and place constraints upon, the kinetics of $\dot{V}O_2$ during exercise. ... We suggest that only by appreciating how the 'traditional' parameters of physiological function interact with the kinetics of $\dot{V}O_2$ can the physiological determinants of athletic performance be truly understood".

This 'contemporary' viewpoint (Burnley & Jones, 2007) claims that the characteristics of the $\dot{V}O_2$ kinetics (Tschakovsky & Hughson, 1999) that describe the time course of $\dot{V}O_2$ at onset of exercise (or to a larger extent during any increase in intensity)- determine the 'intensity domains' (Figure 2) and therefore the rate of changes (accumulation / storage / utilisation) in the 'traditionally'-described limiting factors of performance (Figure 3).

Domain	Boundaries	$\dot{V}O_2$ kinetic responses	Endurance time	Likely fatigue mechanisms
Moderate	Upper: LT	Two components; steady state achieved within 3 min in healthy individuals	>4 h	Hyperthermia (in the heat), reduced central drive/motivation ("central fatigue"), muscle damage (running)
Heavy	Lower: LT Upper: CP	Three components; slow component evident after primary phase; steady state delayed by 10–20 min; elevated $\dot{V}O_2$	Up to ~3–4 h	Glycogen depletion, hyperthermia
Severe	Lower: CP Upper: highest power that elicits $\dot{V}O_{2max}$ before fatigue	Two/three components; slow component evident that develops continuously if power below $\dot{V}O_{2max}$; no steady state; $\dot{V}O_{2max}$ attained if sustained	Up to ~30–45 min	Depletion of finite energy store represented by W' or the oxygen deficit and/or accumulation of fatiguing metabolites (e.g. H^+ , $H_2PO_4^-$)
Extreme	Lower: highest power eliciting $\dot{V}O_{2max}$	Two components; no slow component evident; $\dot{V}O_{2max}$ not attained	<120 s	As for severe + excitation – contraction coupling failure

Note: LT = lactate threshold; CP = critical power.

Figure 2. The 'intensity domains' (Burnley & Jones, 2007).

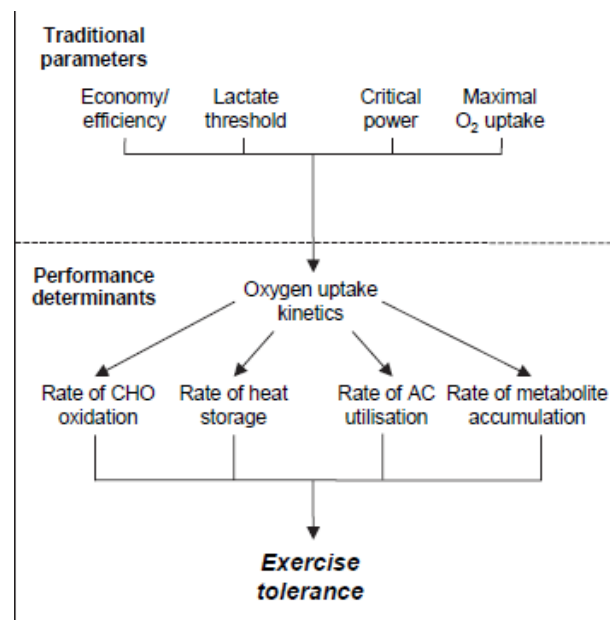


Figure 3. The role of $\dot{V}O_2$ kinetics in heavy- and severe-intensity exercise tolerance (Burnley & Jones, 2007) (Key: CHO carbohydrate, AC anaerobic capacity).

It is surprising that there are very few studies describing or comparing $\dot{V}O_2$ kinetics in triathletes.

1. TRAINING CHARACTERISTICS OF LD VS OD TRIATHLETES

Given the different race intensity and durations of OD and LD racing, and the fact that athletes increasingly tend to specialise in one or the other competition, it is logical that significant training (and therefore, physiological) differences, should exist between type of the two groups. Surprisingly, however, little examination of the way that LD vs. OD triathletes train has been carried out. Table 1 (overleaf) summarises the results of the only comparative study that exists to date (Vleck et al., 2009; Vleck, 2010).

Essentially, OD athletes spend less time per week than LD athletes doing 'long run' ($p < 0.05$ for both genders) and 'long bike' sessions ($p < 0.05$, for females only). The length of individual such sessions is also less in OD than LD athletes in ($p < 0.05$). Squad OD athletes also do more speed work cycle and less long run sessions per week (both $p < 0.05$). Less elite OD athletes do back to back cycle run training than LD athletes ($p < 0.05$).

Table 1. Training characteristics of British (1994) National Squad triathletes during a typical race training week without taper.

		Elite male OD	Sub-elite male OD	Elite male IR	Elite OD female	Sub-elite OD female	Female IR elite
Number of sessions per week	Long bike	1.1 ± 1.3	1.2 ± 1.1	1.5 ± 1.5	1.5 ± 0.6	1.4 ± 1.6	2.3 ± 1.3
	Hill rep bikes	0.3 ± 0.5*	0.2 ± 0.4	0.3 ± 0.5	1.2 ± 1.1*	0.6 ± 0.5	0.5 ± 1.0
	Speed work bike	1.5 ± 1.0	2.1 ± 1.0	1.5 ± 1.0	2.1 ± 1.0	1.0 ± 0.6	0.5 ± 0.6
	Other bike	1.1 ± 1.3	1.1 ± 1.1	1.5 ± 1.5	0.5 ± 0.6	1.4 ± 1.6	2.3 ± 1.3
	Long run	0.7 ± 0.5	0.7 ± 0.5 [⊗]	1.0 ± 0.7 [⊗]	0.8 ± 0.5	0.7 ± 0.5	0.8 ± 0.5
	Hill rep run	0.3 ± 0.5	0.3 ± 0.4	0.3 ± 0.6	0.25 ± 0.5	0.0	0.5 ± 0.58
	Speed work run	1.2 ± 0.8	1.5 ± 1.2	1.1 ± 0.5	1.0 ± 0.0	1.6 ± 0.8	1.0 ± 0.0
	Other run	2.0 ± 2.0	2.2 ± 1.3	2.2 ± 1.7	1.0 ± 0.0	1.4 ± 0.8	1.5 ± 0.6
Hours per week	Long bike	3.2 ± 2.6	3.1 ± 2.7	4.7 ± 1.8	2.45 ± 1.4*	2.25 ± 1.8	5.8 ± 1.7*
	Hill rep bike	0.3 ± 0.7	0.1 ± 0.4	0.8 ± 0.9	0.7 ± 0.8	0.0	0.0
	Speed work bike	1.2 ± 0.7	1.3 ± 1.0	1.1 ± 0.8	1.45 ± 1.0	5.95 ± 10.7	1.0 ± 0.8
	Other bike	1.6 ± 1.6	1.4 ± 1.7	2.4 ± 3.0	0.9 ± 0.9	1.5 ± 0.4	2.6 ± 1.0
	Long run	1.3 ± 1.0 [⊗]	0.4 ± 0.6 [⊗]	1.6 ± 0.7	0.7 ± 0.6	0.2 ± 0.3 [⊕]	2.2 ± 0.3 [⊕]
	Hill rep run	0.4 ± 0.5	0.2 ± 0.3	0.8 ± 0.9	0.2 ± 0.5	0.0	0.5 ± 0.6
	Speed work run	0.8 ± 0.6	1.0 ± 1.0	0.9 ± 0.7	0.8 ± 0.6	1.13 ± 1.0	0.87 ± 0.1
	Other run	1.2 ± 0.9	1.0 ± 1.3	0.5 ± 0.4 ^x	0.6 ± 0.6	1.5 ± 0.6	1.3 ± 0.6 ^x
Distance (km)	Long bike	105.0 ± 75.7	80.5 ± 52.5	52 ± 73.5	68.5 ± 29.3	86.2 ± 43.0	116.0 ± 31.8
	Hill rep bike	-	-	8.0 ± 11.3	11.8 ± 17.8	16.6 ± 19.3	0.0
	Speed work bike	49.5 ± 24.6	47.7 ± 33.3	28.0 ± 17.0	16.0 ± 17.0	29.0 ± 21.5	8.0 ± 13.9
	Other bike	54.1 ± 83.6	53.8 ± 78.2	0	36.9 ± 34.8	24.1 ± 33.2	24.3 ± 24.0
	Long run	16.8 ± 15.1	10.9 ± 11.5	12.0 ± 17.0	12.0 ± 7.0	14.9 ± 6.5	20.1 ± 6.4
	Hill rep run	5.6 ± 7.8 [°]	2.5 ± 4.2	0.0 [°]	2.5 ± 4.2	1.5 ± 4.2	1.0 ± 1.7
	Speed work run	6.5 ± 6.3	9.8 ± 8.1	8.3 ± 10.9	8.6 ± 9.1	7.7 ± 5.0	9.2 ± 6.0
	Other run	-	10.3 ± 7.1	24.6 ± 19.0	17.4 ± 15.5	4.6 ± 5.6	7.3 ± 4.8

Abbreviations: 'OD' Olympic distance, 'IR' Ironman distance

⊗, ⊕, *, †, °, or ⊙ significantly different value ($p < 0.02$) from group marked with same symbol.

*, †, ‡, or ∘ significantly different value ($p < 0.05$) from group marked with same symbol.

Data on weekly training volume in hours (Table 2) or mileage (Table 3), that are differentiated by competitive distance, ability level and or gender, are scarce. Retrospective studies investigating whether training content has increasingly diverged between OD and LD triathletes, since the 1980's, would be of interest and potentially allow for better understanding of the extent to which the sport has changed over the past 30 years.

Table 2. Weekly training time (h).

N	Sex	Ability	Dist.	Total/wk (h)	Swim/wk	Cycle/wk	Run/wk	Reference(s)
21	M	Elite	Short	17.4	5.6	6.3	3.7	Millet et al., 2002; Chatard et al., 1998; Vleck et al., 2010
20	F			13.4	3.7	6.6	3.0	Millet et al., 2002; Vleck et al., 2010; Laurenson et al., 1993
46	M	Comp	Short	14.0	4.04	4.9	2.7	Caillaud et al., 1995 ; Delextrat et al., 2003
20	F			7.5	4.3	8.2	2.0	Vleck et al., 2010; Laurenson et al., 1993
60	M	Comp	Long	18.53	3.4 ± 1.4	8.3 ± 2.8		Farber et al., 1987; Whyte et al., 2000
12		Elite		19.5 ± 7.6	6.1 ± 4.5	8.8 ± 4.5	3.9 ± 1.7	Vleck et al., 2010
25	F	Comp		14.52	3.20 ± 1.78	5.70 ± 1.93		Farber et al., 1987; Leake & Carter, 1991
7		Elite		18.5 ± 2.5	4.2 ± 0.6	3.8 ± 0.9	10.3 ± 2.3	Vleck et al., 2010; Whyte et al., 2000

Table 3. Triathlon training distance (km).

N	Sex	Level	Dist.	Total /wk	Swim/wk	Cycle/wk	Run/wk	Reference(s)
45	M	E	Short	-	13.67	255.82	38.99	Millet et al., 2002; Vleck et al., 2010; Chapman et al., 2008; Chollet et al., 2000; Hue et al., 2000; Schneider et al., 1990; Schneider & Pollack, 1991
121		C		19.1	12.0	201.1	43.0	Vleck et al., 2010; Hue et al., 2000; Bernard et al., 2003; Boussana et al., 2000; Boussana et al., 2001; De Vito et al., 1995; Deitrick, 1991; Delextrat et al., 2003; Hausswirth et al., 1997; Hausswirth et al., 2001; Hausswirth et al., 2000; Hue et al., 1998; Rowbottom et al., 1997; Vercruyssen et al., 2005; Vleck & Garbutt, 1998
20	F	E		187.8±69.4	12.2	180.4	54.6	Millet et al., 2002; Vleck et al., 2010; Laurenson et al., 1993
33		C		194.4±43.2	9.5	74.32	27.78	Vleck et al., 2010; Laurenson et al., 1993; Danner & Plowman, 1995
22	M	E	Long	200.7±136.7	16.4	178.9	186.2	Vleck et al., 2010; Holly et al., 1986
97		C			10.2	326.8	58.7	Holly et al., 1986; Sagnol et al., 1990
7		E		196.9±67.3	11.0±3.0	148.3±61.7	37.5±112.3	Vleck et al., 2010
26	F	C			9.8	353.4	72.4	Holly et al., 1986; Massimino et al., 1998

Key: M male F female E Elite C Competitive L low

2. MAXIMAL AEROBIC POWER AND THE ANAEROBIC THRESHOLD IN OD AND LD TRIATHLETES

2.1 Maximal aerobic power

Table 4 shows the studies that have reported maximal oxygen uptake and peak work load or power for cycling and running in triathletes (Basset & Boulay, 2000; Hue, Le Gallais, Chollet, Prefaut, 2000; Schneider, Lacroix, Atkinson, Troped, Pollack, 1990; Kreider, 1988; Hue, Le Gallais, Chollet, Boussana, Prefaut, 1998; Vercruyssen, Suriano, Bishop, Hausswirth, Brisswalter, 2005; Albrecht, Foster, Dickinson, 1986; Kohrt, Morgan, Bates, Skinner, 1987; O'Toole, Hiller, Crosby, Douglas, 1987; O'Toole, Hiller, Douglas, 1987; Roalstad, 1989; Flynn, Costill, Kirwan, Fink, Dengel, 1987; Kreider, Boone, Thompson, Burkes, Cortes, 1988; Loftin, Warren, Zingraf, Brandon, Skudlt, 1988; Dengel, Flynn, Costill, Kirwan, 1989; Stein, Hoyt, Toole, Leskiw, Schluter, Wolfe, et al., 1988; Kohrt, O'Connor, Skinner, 1989; Millard-Stafford, Sparling, Roskopf, Hinson, DiCarlo, 1990; Rehrer, Brouns, Beckers, ten Hoor, Saris, 1990; Butts, Henry, McLean, 1991; Deitrick, 1991; Medelli, Maingourd, Bouferrache, Bach, Freville, Libert, 1993; Sleivert & Wenger, 1993; Miura & Ishiko, 1993; Murdoch, Bazzarre, Snider, Goldfarb, 1993; Miura, Kitagawa, Ishiko, Matsui, 1994; Zhou, Robson, King, Davie, 1997; Roberts & McElligott, 1995; Ruby, Robergs, Leadbetter, Mermier, Chick, Stark, 1996; Kerr, Trappe, Starling, Trappe, 1998; Derman, Hawley, Noakes, Dennis, 1996; Miura, Kitagawa, Ishiko, 1997; Hue, Le Gallais, Boussana, Chollet, Prefaut, 1999; Miura, Kitagawa, Ishiko, 1999; Schabort, Killian, St Clair Gibson, Hawley, Noakes, 2000; Hue, Le Gallais, Boussana, Chollet, Prefaut, 2000; Toraa & Friemel, 2000; Hue, Le Gallais, Boussana, Galy, Chamari, Mercier, et al., 2000; Hue, Le Gallais, Prefaut, 2001; Hue, Galy, Le Gallais, Prefaut, 2001; Vercruyssen, Brisswalter, Hausswirth, Bernard, Bernard, Vallier, 2002; Basset & Boulay, 2003).

Kohrt et al. (1987) and O'Toole et al. (1987) were among the first groups of researchers to compare $\dot{V}O_{2\max}$ of triathletes measured in both cycle ergometry and treadmill running. In 13 LD triathletes, they found that $\dot{V}O_{2\max}$ was significantly lower in cycle ergometry as compared with treadmill running (57.9 ± 5.7 vs. 60.5 ± 5.6 ml·kg⁻¹·min⁻¹). In contrast, O'Toole et al. (1987) reported similar $\dot{V}O_{2\max}$ values for treadmill running and cycling. Therefore, the data were inconclusive as regards differences in $\dot{V}O_{2\max}$ between cycling and running in triathletes. Although said data were obtained during the 'early ages' of LD triathlon, however, they still appear to be valid.

Similarly, it seems that OD triathletes exhibit similar values for $\dot{V}O_{2\max}$ in cycling and running (Hue, Le Gallais, Chollet, Prefaut, 2000; Sleivert & Wenger, 1993; Zhou, Robson, King, Davie, 1997). In another study, Miura et al. (1999) examined two groups of triathletes whom they characterised as 'superior' or 'slower' level. They found no significant difference in $\dot{V}O_{2\max}$ in cycling and running in both groups. Therefore, any differences in $\dot{V}O_{2\max}$ between exercise modes may not be due to ability level. However, Schabort et al. (2000) found $\dot{V}O_{2\max}$ to be significantly higher in treadmill running than cycle ergometry (68.9 ± 7.4 vs. 65.6 ± 6.3 ml·kg⁻¹·min⁻¹) in national level triathletes. Most studies have also shown that $\dot{V}O_{2\max}$ is similar (i.e. with less than a 7% difference, or approximately the 5 ml·kg⁻¹·min⁻¹ of estimated methodological error that occurs during measurement of $\dot{V}O_{2\max}$) in cycling and running for triathletes over a wide range of competitive levels (Hue, Le Gallais, Chollet, Prefaut, 2000; Dengel, Flynn, Costill, Kirwan, 1989; Medelli, Maingourd, Bouferrache, Bach, Freville, Libert, 1993; Sleivert & Wenger, 1993; Zhou, Robson, King, Davie, 1997; Miura, Kitagawa, Ishiko, 1997).

A schematic of the differences in $\dot{V}O_{2\max}$ between cycling and running in triathletes is provided below (Figure 4). It emphasises that multi-sport training induces a profile that is intermediate to that of runners or cyclists.

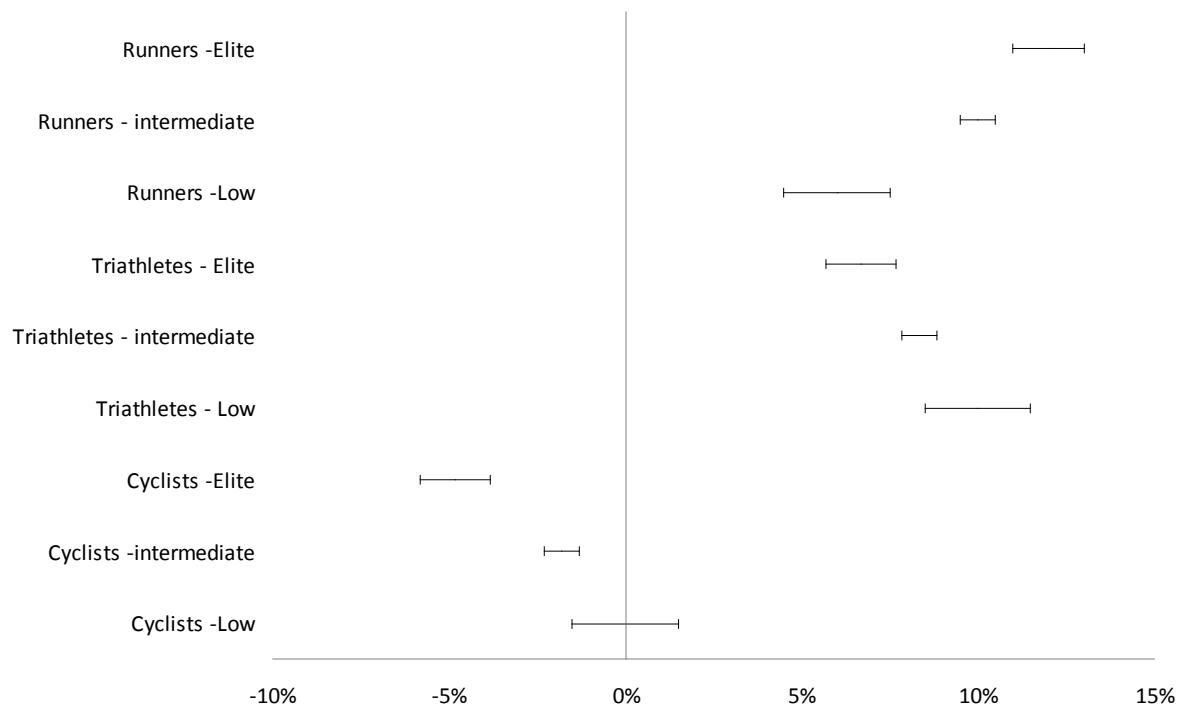


Figure 4. Differences between running and cycling: $\dot{V}O_{2max}$.

2.2 Anaerobic threshold

Despite the fact that controversy still exists regarding the validity of the AT, a number of authors in the field of triathlon research have extended on initial studies by comparing both $\dot{V}O_{2max}$ and a measure of the AT in cycling and running in triathletes (Hue, Le Gallais, Chollet, Prefaut, 2000; Schneider, Lacroix, Atkinson, Troped, Pollack, 1990; Sleivert & Wenger, 1993; Schneider & Pollack, 1991; O'Toole & Douglas, 1995). Table 5 shows the ventilatory or anaerobic threshold data in cycling and running in OD and LD triathletes (Withers, Sherman, Miller, Costill, 1981; Hue, Le Gallais, Chollet, Prefaut, 2000; Schneider, Lacroix, Atkinson, Troped, Pollack, 1990; Bernard, Vercruyssen, Grego, Hausswirth, Lepers, Vallier et al., 2003; Hue, Le Gallais, Chollet, Boussana, Prefaut, 1998; Vercruyssen, Suriano, Bishop, Hausswirth, Brisswalter, 2005; Albrecht, Foster, Dickinson, 1986; Sleivert & Wenger, 1993; Zhou, Robson, King, Davie, 1997; Roberts & McElligott, 1995; Miura, Kitagawa, Ishiko, 1999; Vercruyssen, Brisswalter, Hausswirth, Bernard, Bernard, Vallier, 2002; Schneider & Pollack, 1991; Davis, Vodak, Wilmore, Vodak, Kurtz, 1976; Jacobs & Sjodin, 1985; Miura, Kitagawa, Ishiko, 1994; Moreira-da-Costa, Russo, Picarro, Silva, Leite-de-Barros-Neto, Tarasanchi et al., 1984; De Vito, Bernardi, Sproviero, Figura, 1995; Billat, Mille-Hamard, Petit, Koralsztein, 1999; Galy, Hue, Boussana, Peyreigne, Couret, Le Gallais et al., 2003; Millet & Bentley, 2004).

Kohrt et al. (1989) conducted a 6 to 8 month longitudinal investigation of 14 moderately trained LD triathletes. The researchers quantified $\dot{V}O_{2max}$ and the LT in both cycling and running. $\dot{V}O_{2max}$ remained relatively constant in both cycling and running until the latter stages of the training period, possibly reflecting an increase in training intensity at that time. However, $\dot{V}O_{2max}$ together with the LT in cycling was consistently lower than that obtained for treadmill running. This suggests that the subjects' training background was more extensive in cycling than running. This study also indicates that the nature of training in either exercise mode may influence adaptation in cycling or running. In a more recent longitudinal study (Galy, Manetta, Coste, Maimoun, Chamari, Hue, 2003) taking over one season in trained OD triathletes, the relative stability of $\dot{V}O_{2max}$ and the larger change in VT under the influence of specific training was confirmed. However, Albrecht et al. (1986) found no difference between the VT (expressed as % $\dot{V}O_{2max}$) obtained in cycling (78.8%) or running

(79.3%). In accordance with this, Kreider (1988) showed no significant difference in the VT in triathletes completing incremental tests in cycling and treadmill running.

Interestingly, the latter authors found that the exercise intensity sustained during the cycle and running stages of a OD triathlon was similar. In single sport endurance competitions it is generally thought that the AT reflects the ability to sustain a set percentage of maximum capacity (Bassett & Howle, 2000). Kreider's data (2000), collected for a triathlon event, imply otherwise. Despite the VT of the athletes occurring at a different exercise intensity within isolated incremental running and cycling tests (90 vs. 85% of $\dot{V}O_2\text{max}$), the exercise intensity that they sustained during a race was similar for both exercise modes. However, De Vito et al. (1992) showed the VT in running to be lower after prior cycle exercise in OD triathlon. These results and those reported by Zhou et al. (1997) suggest that the cycle stage of a OD triathlon influences the ability to sustain a set percentage of maximal capacity during the subsequent running stage.

Miura et al. (1999) also reported VT measured in cycling and running to be similar, in absolute terms, in two groups of triathletes who varied in OD triathlon race time. Schneider et al. (1990) was able to confirm these findings and found that whilst $\dot{V}O_2\text{max}$ was significantly higher in running when compared with cycle exercise (75.4 ± 7.3 vs. 70.3 ± 6.0 ml·kg⁻¹·min⁻¹), the VT was not significantly different between cycling and running when expressed as an absolute $\dot{V}O_2$ value but did differ relative to $\dot{V}O_2\text{max}$ (66.8 ± 3.7 vs. $71.9 \pm 6.6\%$).

2.3 Heart rate

In triathletes, the maximal heart rate (HR_{max}) observed in cycling is often lower by 6-10 b·min⁻¹ than that obtained during running (Hue, Le Gallais, Chollet, Boussana, Prefaut, 1998; Kohrt, O'Connor, Skinner, 1989; Hue, Le Gallais, Boussana, Chollet, Prefaut, 1999; Roecker, Striegel, Dickhuth, 2003). Longitudinal investigations have demonstrated HR_{max} to remain relatively stable over the course of a season (Galy, Manetta, Coste, Maimoun, Chamari, Hue, 2003), with higher values (~5 b·min⁻¹) observed in running than in cycling (Kohrt, O'Connor, Skinner, 1989). In contrast, there is also evidence suggesting that HR_{max} is similar between cycling and running modes (Kohrt, Morgan, Bates, Skinner, 1987; Medelli, Maingourd, Bouferrache, Bach, Freville, Libert, 1993; Zhou, Robson, King, Davie, 1997; Basset & Boulay, 2003; Bassett & Howley, 2000). Although this appears to hold for males, differences were observed for this variable in females by some authors (O'Toole, Hiller, Douglas, 1987). Schneider and Pollack (1991), however, found no such significant differences between cycling and running HR_{max} in elite female triathletes.

The HR corresponding to the AT is used to prescribe submaximal exercise training loads (O'Toole, Douglas, Hiller, 1998; Gilman, 1996). The data concerning triathletes indicate that the HR corresponding to certain inflection points associated with the AT is always higher in running than cycling, both when expressed in absolute terms and relative to HR_{max} (Schneider, Lacroix, Atkinson, Troped, Pollack, 1990; Hue, Le Gallais, Chollet, Boussana, Prefaut, 1998; Zhou, Robson, King, Davie, 1997; Hue, Le Gallais, Boussana, Chollet, Prefaut, 1997; Schneider & Pollack, 1991; Roecker, Striegel, Dickhuth, 2003). Schneider et al. (1990) reported a significant difference in the HR corresponding to the VT in cycling and running (145.0 ± 9.0 vs. 156.0 ± 8.0) in 'highly trained' triathletes. This corresponded to 80.9 ± 3.4 vs. $85.4 \pm 4.1\%$ HR_{max} . In another study by the same research group and conducted on elite female triathletes (Schneider & Pollack, 1991), a higher HR was recorded at the VT in running than in cycling (164.7 ± 4.0 vs. 148.2 ± 3.4) and this difference was also evident when HR was expressed as a % of HR_{max} (87.3 ± 1.6 vs. $79.7 \pm 1.5\%$). Similarly, Roecker et al. (2003) found a difference of 20 b·min⁻¹ between HR determined at the LT on cycling ergometer (149.9 ± 18.0 b·min⁻¹) and treadmill (169.6 ± 15.7 b·min⁻¹). However, recreational subjects (~ 22 b·min⁻¹) and cyclists (~ 14 b·min⁻¹) exhibited lower differences than triathletes and runners. Additionally, the differences were not influenced by gender.

There is some evidence that HR may not differ between cycling and running. Basset and Boulay (2000) have reported that the relationship between HR and % $\dot{V}O_2\text{max}$ did not differ when calculated either from a treadmill or from a cycle ergometer test. These authors showed also that HR was similar between running and cycle

ergometer tests throughout the training year and concluded that triathletes could use a single mode of testing for prescribing their training HR in running and cycling throughout the year (Basset & Boulay, 2003).

Zhou et al. (1997) showed that the HR corresponding to the VT was significantly higher in running (174.6 ± 4.5) as compared with cycling (166.4 ± 7.6). However these authors found that the HR measured in a OD triathlon race was similar to the HR at the VT in cycling but much lower in running. Other studies have also shown a decrease in the HR_{max} and the HR corresponding to the VT during an incremental running test performed after submaximal cycling (Hue, Le Gallais, Boussana, Chollet, Prefaut, 2000). Hue et al. (1998) have also demonstrated that the HR during a 10 km run after 40 km of cycling is higher when compared with the same run without cycling. Therefore, even though the HR corresponding to the AT or HR_{max} may be similar in running compared with cycling (in exercise tests performed in isolation), the HR corresponding to the AT determined from an incremental running test may be different to that observed in a race situation, especially in running. At elite level, due to the stochastic pace, there is no demand to control the exercise intensity for the run in OD triathlon via HR. Within LD triathlon, the potential use of HR for controlling the running pace might be of interest, at least at the beginning of the marathon. However, to our knowledge there is no published protocol for determining HR for this purpose. Furthermore, the effect of prior cycling on HR during running should be considered when prescribing HR during running training on its own.

2.4 Running economy

Running economy can be defined by the $\dot{V}O_2$ (in $ml\ O_2 \cdot kg^{-1} \cdot min^{-1}$) of running at a certain speed, and is usually expressed by the energy cost (EC) of running a distance of one km (in $ml \cdot kg^{-1} \cdot km^{-1}$) calculated as $\dot{V}O_2$ divided by the velocity. EC has been reported in triathletes within both the conditions of isolated running and 'triathlon running' (Millet, Dreano, Bentley, 2003; Hue, Le Gallais, Chollet, Boussana, Prefaut, 1998; Kreider, Boone, Thompson, Burkes, Cortes, 1988; Dengel, Flynn, Costill, Kirwan, 1989; Millet & Bentley, 2004; Hausswirth, Bigard, Berthelot, Thomaidis, Guezennec, 1996; Hausswirth, Bigard, Guezennec, 1997; Hausswirth, Brisswalter, Vallier, Smith, Lepers, 2000; Hausswirth & Lehenaff, 2001; Guezennec, Vallier, Bigard, Durey, 1996; Millet, Millet, Hofmann, Candau, 2000; Boone & Kreider, 1986). It is generally reported that in trained OD triathletes, EC measured at the end of the event is higher by ~10% when compared to isolated run; e.g. 224 vs. 204 $ml \cdot kg^{-1} \cdot km^{-1}$ (Guezennec, Vallier, Bigard, Durey, 1996); 224 vs. 207 $ml \cdot kg^{-1} \cdot km^{-1}$ (Hausswirth, Bigard, Berthelot, Thomaidis, Guezennec, 1996). It has also been reported that the extent of any change in EC subsequent to an exhaustive cycling bout is influenced by athlete performance level, event distance, gender, and age. The effect of a fatiguing cycling bout on the subsequent running energy cost was different between elite ($-3.7 \pm 4.8\%$, when compared to an isolated run) and middle-level ($2.3 \pm 4.6\%$) triathletes (Millet, Millet, Hofmann, Candau, 2000). Elite LD triathletes had slightly (but not significantly) lower EC than OD triathletes (163.8 vs. 172.9 and 163.0 vs. 177.4 $ml \cdot kg^{-1} \cdot km^{-1}$ during an isolated and a 'triathlon' run, respectively) (Millet, Dreano, Bentley, 2003). Surprisingly, no difference has been observed in EC between elite junior and senior triathletes, whether male or female, during an isolated run and a 'triathlon' run (173-185 $ml \cdot kg^{-1} \cdot km^{-1}$) (Millet & Bentley, 2004). However, the increase in EC subsequent to cycling was higher in juniors than in seniors in females (5.8 vs. -1.6%), but not in males (3.1 vs. 2.6%) (Millet & Bentley, 2004).

The mechanisms underlying the deterioration in economy in the 'triathlon run' when compared to isolated run are various: both reported changes in the ventilatory pattern (Hue, Le Gallais, Boussana, Chollet, Prefaut, 1999) leading to a higher $\dot{V}O_2$ of the respiratory muscles (Millet, Millet, Hofmann, Candau, 2000; Millet & Vleck, 2000), and neuromuscular alterations reducing the efficiency of the stretch-shortening-cycle (Hausswirth, Brisswalter, Vallier, Smith, Lepers, 2000; Millet, Millet, Hofmann, Candau, 2000; Millet, Millet, Candau, 2001) have been proposed. Some metabolic factors such as shift in circulating fluids, hypovolaemia and increase in body temperature have also been suggested (Hausswirth, Bigard, Berthelot, Thomaidis, Guezennec, 1996; Hausswirth & Lehenaff, 2001; Guezennec, Vallier, Bigard, Durey, 1996). Of interest are the studies of Hausswirth et al. (1997, 2000, 2001), comparing EC at the end of OD triathlon and at the end of a marathon of similar duration: EC was more increased during marathon (+11.7%) than during OD triathlon (+3.2%) running when compared to an 45-min isolated run. The differences are due mainly to higher decrease

in body weight related to fluid losses, a larger increase in core temperature during the long run and significant mechanical alterations during the long run when compared to the running part of a triathlon.

Interestingly, recent values of EC in World-level distance runners have been reported (Jones, 2006; Lucia, Esteve-Lanao, Olivan, Gomez-Gallego, San Juan, Santiago, et al., 2006; Lucia, Olivan, Bravo, Gonzalez-Freire, Foster, 2007). Jones (2006) showed a continuous decrease in EC of Paula Radcliffe, the current world record holder for the Women's marathon between 1992 ($\sim 205 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$) and 2003 ($\sim 175 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$) corresponding to a 15% improvement whereas $\dot{V}\text{O}_2\text{max}$ ($\sim 70 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$) and body mass ($\sim 54 \text{ kg}$) remained unchanged over the period. Jones reported also that Radcliffe's EC was more recently measured at $165 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$. Billat et al. (2003, 2001) reported higher values in elite female Portuguese and French ($196 \pm 17 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$) (Billat, Demarle, Slawinski, Paiva, Koralsztein, 2001) or Kenyan ($208 \pm 17 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$) (Billat, Lepretre, Heugas, Laurence, Salim, Koralsztein, 2003) distance runners. Overall, this compares favourably with values obtained for elite female triathletes: Millet and Bentley (2004) reported, for nine elite females (including one LD world champion, second at the Hawaii Ironman and five European medallists) an average value of $176.4 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$, whereas the average $\dot{V}\text{O}_2\text{max}$ was $61.0 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ for a body mass of 60.3 kg .

In males, Lucia et al. (2006, 2007) reported a value of $150\text{--}153 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ in Zersenay Tadese, the current long cross-country and half-marathon World champion for a $\dot{V}\text{O}_2\text{max}$ of $83 \text{ ml}\cdot\text{min}^{-1}\cdot\text{kg}^{-1}$. The EC of Tadese is lower (the lowest reported so far) than previously reported values in elite runners: $180 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ for Steve Scott (1984); $203\text{--}214 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ in elite French and Portuguese (Billat, Demarle, Slawinski, Paiva, Koralsztein, 2001) or Kenyan (Billat, Lepretre, Heugas, Laurence, Salim, Koralsztein, 2003) runners; $\sim 190\text{--}192 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ in Elite East-African runners (Lucia, Esteve-Lanao, Olivan, Gomez-Gallego, San Juan, Santiago, et al., 2006; Saltin, Larsen, Terrados, Bangsbo, Bak, Kim, et al., 1995); $\sim 211 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ in Elite Spanish runners (Lucia, Esteve-Lanao, Olivan, Gomez-Gallego, San Juan, Santiago, et al., 2006). So, similarly to females, with the exception of Tadese, running economy in male distance runners does not appear to be better than the ones reported in elite triathletes: 174 ± 9 and $164 \pm 8 \text{ ml}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ for OD and LD triathletes, respectively (Millet, Dreano, Bentley, 2003). However further investigation with Elite LD triathletes is required to confirm these results. Overall, from these data, it appears that the main difference in running performance between elite runners and triathletes comes mainly from a higher body mass in triathletes (affecting proportional $\dot{V}\text{O}_2\text{max}$) rather from differences in running economy. Since mean lower leg thickness and calf mass have been shown to be related to running economy (Saltin, Kim, Terrados, Larsen, Svedenhag, Rolf, 1995), one may speculate that the higher body mass in triathletes comes mainly from the upper body muscles more and – probably – from the higher skinfold thicknesses that are associated with swimming.

2.5 $\dot{V}\text{O}_2$ kinetics

As previously mentioned, in contrast to other endurance sports; i.e. running (Kilding, Fysh, Winter, 2007; Carter, Jones, Barstow, Burnley, Williams, Doust, 2000), cycling (Carter, Jones, Barstow, Burnley, Williams, Doust, 2000), rowing (Ingham, Carter, Whyte, Doust, 2007) or swimming (Reis, Millet, Malatesta, Roels, Borrani, Vleck, et al., 2010) where $\dot{V}\text{O}_2$ kinetics has been well-investigated, only a few studies report $\dot{V}\text{O}_2$ kinetics parameters in triathletes.

Faster kinetics; i.e. smaller constant time of the primary phase (τ_1), has been associated with improved fatigue tolerance and performance in cycling, running or rowing (Burnley & Jones, 2007; Ingham, Carter, Whyte, Doust, 2007). Caputo et al. (2004) compared trained triathletes, cyclists and runners on both running and cycling maximal exercises. τ_1 was similar between treadmill and cycle ergometer in runners (31.6 and 40.9 s); cyclists (28.5 and 32.7 s) and triathletes (32.5 and 40.7 s). Despite the fact that these authors concluded that $\dot{V}\text{O}_2$ kinetics was not dependent on the exercise mode and specificity of training as in previous studies (Carter, Jones, Barstow, Burnley, Williams, Doust, 2000), one may observe that the triathletes responses were similar to the ones of the runners, for whom the difference between cycling and running was larger than in cyclists.

It seems that in trained subjects, acceleration of the $\dot{V}O_2$ adjustments at the onset of heavy exercise after endurance training is not always observed, in opposition to untrained subjects. For example, Millet et al. (2002) did not report that in a group of already well-trained triathletes, training induces a faster constant time of the primary phase. However, they reported in the seven subjects with the lowest $\dot{V}O_{2\max}$ (~64 mL·min⁻¹·kg⁻¹), that τ_1 decreased from 21 to 14 s.

Comparison of $\dot{V}O_2$ kinetics parameters (as well as running EC and anaerobic capacity in cycling) between OD and LD triathletes appears to be a first priority in the characterisation of training adaptations, and improvement of understanding of the determinants of performance in triathlon, using a "modern" scientific perspective.

3. INJURY DIFFERENCES IN OD AND LD TRIATHLETES

Differences in training adaptations between LD and OD triathletes may, moreover, have implications for the incidence and or severity of overuse injury in these groups. In a preliminary retrospective study, Vleck (2010b; Vleck et al., 2010) found the number of overuse injuries sustained over a five-year period did not differ between OD and LD triathletes. However, the proportions of OD and LD athletes who were affected by injury to particular anatomical sites did ($p < 0.05$). For example, a greater proportion of OD than LD males sustained Achilles tendon injury ($p < 0.05$). In addition more of the total number of overuse injuries that were sustained by OD athletes occurred to the lower back (17.9%), Achilles tendon (14.3%) and knees (14.2%), whilst most of the injuries that were reported by LD athletes were to the knees (44%), calf (20%), hamstrings (20%) and lower back (20%). Moreover, less OD athletes (16.7% vs. 36.8%, $p < 0.05$) reported their injury to recur. Although OD sustained less running injuries than LD (1.6 ± 0.5 vs. 1.9 ± 0.3 , $p < 0.05$), more subsequently stopped running (41.7% vs. 15.8%), and for longer (33.5 ± 43.0 vs. 16.7 ± 16.6 days, $p < 0.01$). In OD, the number of overuse injuries sustained inversely correlated with percentage training time, and number of sessions, doing bike hill repetitions ($r = -0.44$ and -0.39 , respectively, both $p < 0.05$). LD overuse injury number correlated with the amount of intensive sessions done ($r = 0.67$, $p < 0.01$ and $r = 0.56$, $p < 0.05$ for duration of 'speed' run and 'speed bike' sessions). It is important, therefore, that coaches note that the physiological and training differences between OD and LD triathletes may lead to their exhibiting differential risk for injury to specific anatomical sites.

CONCLUSIONS

After 30 years of scientific investigation, we can conclude that only the "traditional / old-fashioned" physiological parameters ($\dot{V}O_{2\max}$, anaerobic threshold) have been measured and analysed on a large-scale. Only a few data are available for running EC or cycling efficiency in triathletes. Almost nothing has been published on anaerobic capacity in cycling or $\dot{V}O_2$ kinetics. Very little is known regarding training content. Research regarding both the extent of, and the risk factors for, injury in LD and OD triathletes, is very much in its infancy (Vleck, 2010).

The International Triathlon Union can be pro-active in initiating a longitudinal assessment of elite triathletes. It will obviously help coaches and scientists. The data so collected may also complement the data collected for the "blood/biological passport" and comprise the first step towards a "physiological passport".

Table 4. Studies that have assessed maximal oxygen uptake for cycling and running in OD and LD

Reference	Sport	N	Level/ Details	Age (yrs)	Mass (kg)	Rel. $\dot{V}O_{2\max}$ bike (ml·kg ⁻¹ ·min ⁻¹)
Albrecht et al., 1986	OD	9 M	Experienced			56.3
Kohrt et al., 1987	LD	13 M	Competitive	29.5±4.8	69.8±5.6	57.9±5.6*
O'Toole et al., 1987	LD	8 M	Ser. amateur (SA)	30.5±8.8	74.7±10	66.7±10.1
		6 F	World-Class (WC)	31.3±5.6	60.3±4.6	61.6±7
		5 F	WC subgroup			67.0±7.7
		1 F	SA subgroup			60.6
		6M	SA subgroup			66.1±9.2
		2 M	WC subgroup			77.0±10.0
O'Toole et al., 1987	LD		Highly trained	30.5±8.8	74.7±10.0	66.7±10.1
				31.3±5.6	58.8±5.7	64.0±8.9
Roalstad, 1989	LD	8 F				56.9
		10 M	Not clear			64.3
Flynn et al., 1987	LD	11 M	Top 200	31.4±5.9	74.5±7.6	
Kreider, 1988	OD	10 M	None given			
Kreider et al., 1989	LD	9 M				64.3±8.5
Loftin et al., 1988	OD	14 M	Competitive			43.6±8.1
Dengel et al., 1989	LD	11 M	Not clear	31.4±1.8	74.5±2.3	63.2±0.1
Stein et al., 1989	OD	4 M	'Elite'			
Kohrt et al., 1989	LD	8 M, 6 F	(I, Feb.)	29.4±5.1	M 55.3-56.4 F 69.9-71.3	53.4±1.5*
			(II, Feb+6-8 wks)			55.5±1.5*
			(III,+6-8 wks)			54.2±1.5*
			(IV, Sept., race)			56.0±1.3*
Schneider et al., 1990	OD	10 M	Highly trained	27.6±6.3	72±5.4	70.3±6*
Millard-Stafford et al., 1990	OD	10 M	Competitive			62.9±3.8
Rehrer et al., 1990	LD	10 M	Not clear			60.8±1.4
Butts et al., 1991	OD	7 F	Recreational			48.2±3.8
		16 M	Not clear			56.5±8.5
Deitrick, 1991	OD	7 M	Competitive			60.5±6.2 ^{MW}
		7 M	Competitive			51.9±3.9 ^{HW}
Medelli et al., 1993	OD	7 M		24±3	75±10	66.4±1
Sleivert & Wenger, 1993	OD	18 M		27.7±1.3	76.2±2.1	51.1±2
		7 F		28.3±2.3	59.3±2.1	60.1±1.5

Reference	Sport	N	Level/ Details	Age (yrs)	Mass (kg)	Rel. $\dot{V}O_2$ max bike (ml·kg ⁻¹ ·min ⁻¹)
Miura & Ishiko, 1993	OD	9 M				57.9±4.5
Murdoch et al., 1993	OD	8 M				67.1±2.6
Miura et al., 1994	OD	14 M				58.5±6.8
Zhou et al., 1997	OD	10 M	Amateur	27.4±5.7	78.4±8	61.3±10.1
Roberts & McElligott, 1995	OD	7 F				54.3±3.6
		7 F				63.2±3.9
Ruby et al., 1996	OD	6 F	10 wks R	20.3±0.9	58.2±3.3	
		6 F	10 wks C	20.5±1.0	61.6±3.6	
		6 F	10 wks C+R	21.3±0.6	62.4±3.0	
Kerr et al., 1998	OD	5 M	Competitive			60.8±3.0
Derman et al., 1996	OD	6 M				
Miura et al., 1997	OD	17 M		26.5±8.2	62.8±5.1	61.1±8.1
Hue et al., 1998	OD	7 M	Competitive	20.8± 2.9	69.7±4.5	65.4±4.2
Hue et al., 1999	OD	9 M				70±4.8
Miura et al., 1999	OD	8 M	Superior	27.3±6.8	65.4±5.8	67.8±6.1 [#]
		8 M	Lower	26±10.3	60.8±3.2	54.9±3.8 [#]
Basset & Boulay, 2000	OD	4 M, 2 F		21.3±1.6	65.7±5.6	64.6±2.6 [*]
	C	6 M		24.3±7.5	72.5±3.7	71.2±3.9 [*]
	R	4 M, 2 F		21.0±2.4	64.8±13.8	61.7±5 [*]
	All	14 M, 2 F		22.2± 5	67.7±9.1	65.8±4.8 [*]
Hue et al., 2000	OD	29 M	Competitive	20.9±2.6	68±7.8	69.1±7.2
		6 M	Elite	21.8±2.4	69.9±7.3	75.9±5.2
Schabort et al., 2000	OD	5 M	National Squad	23±4	72.1±4.7	69.9±4.5 [*]
		5 F		25±7	59.3±5.8	61.3±4.6
		5 M, 5 F				65.6±6.3
Hue et al., 2000	OD	8 M	Competitive			64.7±2.4
			Elite Senior			75.7±2.3
Toraa & Friemel, 1990	OD	12 M	Good level			70.7±3.8
		12 M	Middle-level			67.7±6.4
Hue et al., 2000	OD	13 M	University team			67.2±1.6
Hue et al., 2001	OD	10 M				67.1±1.6
Hue et al., 2003	OD	13 M	Competitive			67.2±1.6
Vercruyssen et al., 2003	OD	8 M	University team	24.0±3.0	71.1±6.5	68.7±3.2
Basset & Boulay, 2003	OD	4 M, 4 F	Preparat. training	22±2	60.7±10	60.9±6.7
			Specific training			61.9±6.4
			Pre-competition			62.8±7.2
Vercruyssen et al., 2005	OD	8 M		28.9±7.4	73.3±6.0	67.6±3.6

Table 5. Studies showing ventilatory / anaerobic threshold related data for cycling and running in

Reference	Sport	Performance Level	N	VT $\dot{V}O_2$ _bike (L·min ⁻¹)	VT $\dot{V}O_2$ _run (L·min ⁻¹)	VT $\dot{V}O_2$ _bike (ml·kg ⁻¹ min ⁻¹)	V (r
Albrecht et al., 1986	T	Experienced	9 M			44.3	
Kreider et al., 1989	T		10 M	3.9*	4.42*		
Schneider et al., 1990	T	Highly Trained	10 M	3.0±0.5*	3.9±0.3*	46.9±4.3	
Schneider & Pollack, 1991	T	Highly trained	10 F	2.2±0.1	2.8±0.1	37.7±1.9	
Sleivert & Wenger, 1993	T		7 F				
	T		18 M				
De Vito et al., 1995	T	Well trained	6 M		3.7±0.4 3.8±0.6 3.7±0.2		
Roberts & McElligott, 1995	T	Elite	7 M				
Zhou et al., 1997	T	Amateur	10 M	4.0±0.2*	4.5±0.2*	52.2±3.2*	
Hue et al., 1998	T	Competitive	7 M			42.5±6.5	
Billat et al., 1999	T	Competitive					
Miura et al., 1999	T	Superior	8 M			48.7±3.8#	
	T	Lower	8 M			39.7±2.9#	
Hue et al., 2000	T	All	29 M	3.0±0.6*	2.6±0.4*	45.1±8.2	
	T	Elite	6 M	3.0±0.6	2.8±0.3	49±10.9	
Vercruyssen et al., 2003	T		8 M				
Bernard et al., 2003	T	Well trained	9 M				
Galy et al., 2003	T	(Pre-comp)	7 M, 1 F	3.7±0.2# ^o		55.8±2.8#	
		(Comp)	7 M, 1 F	3.7±0.2b		55.4±3.3	
		(Post-comp)	7 M, 1 F	3.3±0.2# ^o		49±4.1c#	
Vercruyssen et al., 2005	T		8 M	(LT) 3.8±0.4*	(LT) 4.4±0.5*		

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