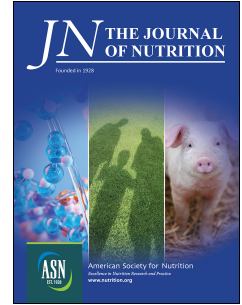


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From Metabolism to Medals: Contemporary Perspectives and Revisiting Carbohydrate Guidelines for Fuelling Endurance Athletes During Exercise

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3 **From Metabolism to Medals:**  
4 **Contemporary Perspectives and Revisiting Carbohydrate Guidelines for Fuelling**  
5 **Endurance Athletes During Exercise**

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39 **Running Head:** CHO recommendations for athletes

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**50 Abstract**

51 The effects of carbohydrate (CHO) intake on substrate metabolism, exercise capacity and  
52 exercise performance have been studied for over 100 years. From a metabolic perspective, the  
53 ergogenic effect of CHO intake is likely mediated by liver (and potentially muscle) glycogen  
54 sparing, maintenance of plasma glucose concentrations and whole-body CHO oxidation rates,  
55 such that the required exercise intensity can be sustained for a longer duration thereby delaying  
56 fatigue. Accordingly, the 2016 sport nutrition guidelines from the American College of Sports  
57 Medicine recommend CHO intakes up to 90 g per hour (from multiple transportable  
58 carbohydrates e.g. glucose/fructose mixtures), as targeted to exercise that is >2.5 to 3 h in  
59 duration. Although field observations report a trend for endurance athletes to consume (and  
60 experiment with) higher rates of CHO ingestion during training and racing (i.e. 120-200 g.h<sup>-1</sup>),  
61 the efficacy of such doses is not yet substantiated by current scientific research. Rather,  
62 contemporary research suggests that the upper limit of CHO intake could increase from 90 to  
63 120 g.h<sup>-1</sup> (at least for trained participants), considering that both exogenous and whole-body  
64 rates of CHO oxidation can be increased with these higher ingestion rates. Such absolute doses  
65 may also modulate important physiological determinants of performance (e.g. durability and  
66 economy) across cycling, marathon running and ultra-endurance exercise. As such, the present  
67 paper provides a contemporary review of CHO metabolism during exercise, factors affecting  
68 exogenous CHO oxidation rates (i.e. CHO blend, ratio, format, environmental considerations  
69 etc) and sport-specific research (alongside personal author insights from practice), before  
70 presenting an updated and more nuanced model to guide CHO personalisation strategies for  
71 endurance athletes. Directions for future research are also discussed, emphasising the need for  
72 collaborative research to study both male and female athletes during ecologically valid exercise  
73 protocols that better address the real-world fuelling challenges faced by elite athletes.  
74 **Keywords:** glucose, fructose, maltodextrin, cycling, marathon, ultra-endurance

## 75 **1: Introduction**

76 It is now an established practice for endurance athletes to consume carbohydrate (CHO) during  
77 exercise, especially in training and competitive scenarios where the exercise stimulus is  
78 prolonged in duration (i.e. > 1 h duration) and of moderate to high intensity in nature (1). Such  
79 “fuelling” practices are firmly grounded in over 100 years of scientific research, where the  
80 potential effect of CHO availability on “real-world” athletic performance was recognised as  
81 early as the 1920s with field observations from the seminal Boston marathon studies. For  
82 example, in the 1924 race, it was reported that a cohort of male runners presented with  
83 hypoglycaemia upon finishing the race and the researchers also reported “it is extremely  
84 significant that a correlation existed between the blood sugar level and the physical condition  
85 of the runner” (p. 1779) (2). Importantly, hypoglycaemia (and associated symptoms) was  
86 prevented in the 1925 race when the same men consumed additional CHO in the day before  
87 and during the race, with notable improvements in their physical condition and faster race time  
88 (3).

89 With the introduction of the muscle biopsy technique almost 40 years later, our  
90 understanding of CHO metabolism during exercise advanced considerably throughout the late  
91 1960s (4, 5) and 1970s (6-10). Indeed, a series of studies from Scandinavia collectively  
92 demonstrated that a short-term high CHO diet increases muscle glycogen storage, that elevated  
93 pre-exercise muscle glycogen availability enhances exercise capacity and performance, and  
94 that exercise depletes muscle glycogen in an intensity dependent manner. Although the role of  
95 glycogen availability in modulating exercise performance was becoming increasingly  
96 accepted, it was not until the 1980s that research evaluating the effects of CHO ingestion  
97 “during” exercise regained momentum. In this decade, studies adopting prolonged cycling as  
98 the exercise modality demonstrated that the rationale to consume CHO during exercise (at least  
99 from a metabolic perspective) is largely based on the premise of preventing hypoglycaemia

100 and maintaining whole-body rates of CHO oxidation, thereby sustaining exercise intensity and  
101 delaying the onset of fatigue (11-15). Additionally, the use of stable isotopes (e.g., [ $^{13}\text{C}$ ] and  
102 [ $6,6\text{-}^2\text{H}_2$ ] glucose) throughout the 1980s (16, 17) and 1990s (18) also allowed researchers to  
103 quantify the utilisation of the differing CHO pools during exercise (e.g. liver, blood and  
104 muscle), whereas the last twenty years of research transitioned towards evaluating the effects  
105 of different sugars / polymers (e.g. glucose, fructose, sucrose, and maltodextrin etc) on  
106 exogenous rates of CHO oxidation (19-21). Collectively, this accumulating body of research  
107 and developments in the field culminated in the most recent sport nutrition guidelines  
108 (published in 2016) recommending CHO intake during exercise at a rate of 30-90 g per hour,  
109 with the dose and blend largely dependent on exercise duration (22). It is noteworthy, however,  
110 that these guidelines are almost a decade old and in building on previous research (19, 20),  
111 more recent research (23, 24) and anecdotal athlete reports (25) have suggested perceived  
112 benefits from even higher doses of CHO ingestion. In recognition of this apparent “fuelling  
113 revolution”, the range of commercial product offerings now available to athletes has grown  
114 considerably, and it remains challenging for athletes, coaches and practitioners to make  
115 evidence-based decisions in relation to optimally fuelling for training and competition.

116         With this in mind, the aim of the present paper is to provide a contemporary review of  
117 CHO fuelling during exercise. In taking a “Metabolism to Medals” approach, we first review  
118 the effects of CHO ingestion on substrate metabolism during exercise, before progressing to  
119 critically evaluate the factors that affect exogenous rates of CHO oxidation and the associated  
120 implications for exercise performance. We then share contemporary research and insights from  
121 applied practice (focusing on cycling, running and ultra-endurance) before presenting more  
122 nuanced CHO guidelines for athletes. Finally, we close by outlining directions for future  
123 research that will hopefully stimulate collaborative research worldwide to collectively address  
124 the “real-world” fuelling challenges continually faced by elite athletes.

## 125 **2: CHO Availability and Substrate Metabolism During Exercise**

### 126 **2.1 Effects of CHO feeding on whole-body substrate metabolism**

127 Our understanding of substrate metabolism during exercise has been progressively advanced  
128 by the collective use of both invasive (e.g. muscle biopsies, isotope tracer infusions) and non-  
129 invasive techniques (e.g. indirect calorimetry, breath stable isotope enrichment, magnetic  
130 resonance imaging and spectroscopy etc), the combination of which has allowed researchers  
131 to evaluate the utilisation of specific substrate pools during differing exercise and nutrient  
132 scenarios. At the whole-body level, it is well documented that the predominant substrates for  
133 energy production during exercise are CHO and fat, where the contribution of each source  
134 towards whole-body energy utilisation is largely determined by the interaction of exercise  
135 intensity (26), duration (27), training status (28) and substrate availability (29). Indeed, such  
136 factors modify the utilisation of both extra-muscular (i.e. adipose tissue derived free fatty acids,  
137 liver glycogen and blood glucose) and intra-muscular sources (i.e. muscle glycogen and intra-  
138 muscular triglyceride), as mediated by hormonal control, cytokine mediated signalling and  
139 allosteric regulation of regulatory enzymes and proteins involved in substrate transport and  
140 metabolism.

141 In the context of evaluating the metabolic effects of CHO feeding “during” exercise, it  
142 is important to consider the nature of the exercise protocol and nutritional conditions of the  
143 chosen experimental design. This is especially relevant when considering that habitual  
144 macronutrient intake (30), pre-exercise muscle glycogen availability (31) and both timing (32)  
145 and composition of the pre-exercise meal (33) can all modify substrate metabolism in favour  
146 of both CHO and fat depending on substrate availability. In an attempt to mimic exercise  
147 conditions that are in accordance with nutritional guidelines and most likely applicable to the  
148 “competitive scenario” of the elite endurance athlete (i.e. 36 h of a high CHO diet and a high  
149 CHO pre-exercise meal), recent research from the first author’s laboratory evaluated the dose

150 dependent effects of CHO intake during exercise on whole-body substrate utilisation (see  
151 Figure 1). Such data demonstrate that CHO feeding (during 3 h prolonged steady state cycling  
152 at 95% of lactate threshold, LT, in trained male cyclists) delays the “crossover point” during  
153 exercise i.e. the time-point during exercise whereby the predominant source of substrate  
154 metabolism shifts from carbohydrate to fat. Moreover, within this given exercise context,  
155 consumption of  $120 \text{ g}\cdot\text{h}^{-1}$  *prevented* the occurrence of the crossover point during exercise (23),  
156 whereas  $90 \text{ g}\cdot\text{h}^{-1}$  only *delays* the time to crossover compared with  $45 \text{ g}$  and  $0 \text{ g}\cdot\text{h}^{-1}$  (34). As  
157 such, it is apparent that CHO dependency during exercise is likely only maintained if CHO  
158 availability, itself, is also maintained, the result of which may have beneficial metabolic (i.e.  
159 economy, efficiency, durability) (35) and performance effects in that the target exercise  
160 intensity and desired race pace may be able to be maintained for a longer duration (14, 36).  
161 However, we acknowledge that a definitive CHO dose response study and its effect on  
162 performance in training or competition related scenarios is yet to be completed under  
163 standardised conditions in the *same* laboratory, as is the case for both male and female athletes.  
164 Nonetheless, in using a multisite trial, Smith, et al. (37) reported a curvilinear dose response  
165 relationship of CHO intake ( $0\text{-}120 \text{ g}\cdot\text{h}^{-1}$ ; 1:1:1 ratio of glucose, maltodextrin, fructose) on  
166 cycling performance (in a cohort of 51 recreationally trained cyclists and triathletes) with  
167 diminishing performance enhancement observed with intakes  $>78 \text{ g}\cdot\text{h}^{-1}$ . In that study, CHO  
168 was ingested during 2 h of cycling at 95% of the workload corresponding to a blood lactate  
169 concentration of  $4 \text{ mmol}\cdot\text{L}^{-1}$  followed by a 20 km time trial. It remains to be proven whether  
170 such dose response relationships are apparent in trained populations and during exercise  
171 scenarios that are more applicable to the intensities and durations associated with other  
172 endurance exercise scenarios.

173

174

## 175 *2.2 Effects of CHO feeding on liver glycogen utilisation and blood glucose*

176 The maintenance of high whole-body CHO oxidation rates associated with CHO ingestion is,  
177 in part, due to a maintenance of high circulating glucose concentrations. In the absence of CHO  
178 ingestion, prolonged moderate-to-high intensity exercise leads to the onset of hypoglycaemia  
179 by ~3 hours (14). The development of hypoglycaemia in this context results from a mismatch  
180 between blood glucose rates of appearance (Ra) and disappearance (Rd), whereby glucose Ra  
181 is insufficient to meet the demands placed by glucose Rd. In the absence of CHO ingestion,  
182 liver glucose output is almost entirely responsible for glucose Ra, with contributions from  
183 hepatic glycogenolysis and gluconeogenesis (38). As exercise duration continues, hepatic  
184 glycogenolysis depletes liver glycogen stores, which would reduce the relative and absolute  
185 contributions of hepatic glycogenolysis to glucose Ra. Since hepatic gluconeogenesis appears  
186 to show little absolute changes with exercise duration or intensity (38, 39), hepatic glucose  
187 output (and consequently glucose Ra) can no longer meet the demand for Rd, and blood glucose  
188 concentrations will decline. For a 75 kg athlete exercising at ~70% of peak oxygen uptake,  
189 hepatic glycogenolysis occurs at approximately 30 g.h<sup>-1</sup> (38). Since the liver has a maximal  
190 capacity to store ~100 g glycogen (38, 40), the onset of hypoglycaemia at 3 hours is consistent  
191 with the occurrence of hepatic glycogen depletion.

192 Accordingly, CHO ingestion during exercise has a profound effect on both delaying  
193 hypoglycaemia and hepatic glycogen depletion. Indeed, as little as 20-30 g.h<sup>-1</sup> of glucose  
194 ingestion may begin to suppress endogenous glucose production and delay the onset of  
195 hypoglycaemia (41, 42). The suppression of endogenous glucose production appears to be  
196 dose-dependent with further suppression of endogenous glucose production up to ingestion  
197 rates of 90-120 g.h<sup>-1</sup> of glucose (41). The suppression of endogenous glucose production  
198 suggests that there may be sparing of liver glycogen contents, which is supported by direct  
199 observations that ingesting large amounts of glucose (~100 g.h<sup>-1</sup>) during exercise can

200 completely prevent liver glycogen depletion (43). Since glucose-fructose mixtures can further  
201 increase CHO availability during exercise (See Section 3.1), it may be surprising that ingesting  
202 glucose-fructose mixtures at  $\sim 100 \text{ g}\cdot\text{h}^{-1}$  does not appear to further increase liver glycogen  
203 concentrations during exercise and instead is likely to be oxidised (43). Indirect estimates have  
204 generally failed to detect differences liver glucose oxidation with increasing CHO ingestion  
205 rates or with differences in CHO type (44, 45), although deduction of exogenous CHO  
206 oxidation from plasma glucose  $R_a$  suggests that glucose-fructose mixtures may reduce  
207 endogenous  $R_a$  during ultra-endurance exercise from  $\sim 0.6$  to  $\sim 0.4 \text{ g}\cdot\text{min}^{-1}$  (46). Therefore, it  
208 currently remains unclear what the dose-response of CHO ingestion during exercise on liver  
209 glycogen sparing is, especially with CHO mixtures, and this information could further inform  
210 fuelling strategies alongside other metabolic and performance data.

211

### 212 ***2.3 Effects of CHO feeding on muscle glycogen utilisation***

213 Although CHO feeding has a clear effect on sparing liver glycogen utilisation during exercise,  
214 effects on muscle glycogen sparing are smaller, more variable at the individual-study level, and  
215 appear to depend on exercise context (e.g., intensity, mode, and the muscle/fibre type assessed).  
216 In running, muscle glycogen sparing has been consistently observed, with relatively modest  
217 CHO intakes (e.g.,  $\sim 60 \text{ g}\cdot\text{h}^{-1}$ ) reported to attenuate mixed and fibre-type specific glycogen  
218 depletion (47, 48). However, many individual studies employing prolonged cycling exercise,  
219 even with ingestion of large amounts (e.g.  $100 \text{ g}\cdot\text{h}^{-1}$ ) of glucose-fructose mixtures, report no  
220 statistically significant reduction in mixed muscle glycogen utilisation compared with placebo  
221 (14, 34, 43). However, a recent meta-analysis of placebo-controlled crossover trials (31 studies;  
222 48 unique effect sizes) indicates that CHO ingestion during prolonged endurance exercise  
223 produces a small but statistically significant muscle glycogen-sparing effect overall  
224 (standardised mean difference  $\sim 0.16$ ), which translates to an estimated sparing of  $\sim 24$

225 mmol·kg<sup>-1</sup> dry wt over ~100 min of exercise (49). Notably, the direction of effect was generally  
226 consistent across studies, and no clear moderators (exercise mode, CHO type, ingestion rate,  
227 or pre-exercise glycogen) were identified. During lower intensity exercise (40% of maximal  
228 power output; ~140 W) muscle glycogen concentrations can even be increased during cycling  
229 exercise when ingesting ~80 g.h<sup>-1</sup> of sucrose (50), although this may not be apparent in  
230 untrained individuals (51). Furthermore, there is indirect evidence that very high CHO  
231 ingestion rates may even stimulate skeletal muscle glycogen utilisation, since tracer methods  
232 demonstrate that increasing glucose ingestion from 60 to 90 g.h<sup>-1</sup> may increase muscle  
233 glycogen oxidation rates during cycling (52). Direct measures of muscle glycogen utilisation  
234 with different doses and mixtures of CHO would provide additional support for this  
235 observation. The effects of CHO ingestion on muscle glycogen utilisation therefore seem to  
236 depend on several factors. Muscle glycogen sparing is more commonly observed during  
237 running than cycling and with lower exercise intensities. Whether the goal is to spare or to  
238 stimulate muscle glycogen use will depend on the competition demands, since in the absence  
239 of reaching critically low muscle glycogen concentrations stimulating muscle glycogen  
240 utilisation may provide greater use of a rapid and oxygen efficient fuel. Furthermore, as  
241 exercise duration is prolonged and muscle glycogen decreases, there is an increasing reliance  
242 on blood glucose oxidation. Therefore, there may be a good rationale to optimise exogenous  
243 CHO availability under these scenarios to improve exercise performance during late stages of  
244 prolonged exercise.

245

#### 246 ***2.4 Effects of CHO feeding on adipose tissue lipolysis and intramuscular triglyceride*** 247 ***(IMTG) utilisation***

248 The magnitude of the exercise-induced reduction in IMTG content (3 h prolonged steady state  
249 cycling in trained male cyclists) in both type I and type IIA fibres is not affected by CHO

250 consumption at rates of 45 or 90 g.h<sup>-1</sup> when compared to 0 g.h<sup>-1</sup>. In contrast, CHO feeding  
251 suppress circulating glycerol and non-esterified fatty acid (NEFA) concentrations in a dose  
252 dependent manner, an effect likely mediated by suppression in hormone sensitive lipase  
253 activity in adipose tissue (53), with decreases in lipolysis and increases in re-esterification . A  
254 dose dependent suppression in circulating NEFA and whole-body lipid oxidation has also been  
255 reported across a smaller range of absolute CHO intake of 0, 20, 39 and 64 g.h<sup>-1</sup>, an effect also  
256 observed in trained male cyclists (during 2 h cycling at 95% of LT) (54). In relation to running,  
257 data from the first author's laboratory also reported that CHO intakes of 60, 90 and 120 g.h<sup>-1</sup>  
258 reduced circulating glycerol, NEFA and whole-body fat oxidation in male trained marathoners  
259 in a dose dependent manner, as demonstrated during a 2 h treadmill running protocol where 90  
260 minutes was completed close to race pace i.e. 94% of lactate turn-point (35). When taken  
261 together, such data demonstrate that the reduction in whole-body fat oxidation associated with  
262 CHO feeding during exercise is most likely related to a reduction in rates of adipose tissue  
263 lipolysis (53) thereby reducing free fatty availability and/or reduced mitochondrial fat transport  
264 (55), as opposed to a reduction in IMTG utilisation (56).

265

266 In summary, CHO ingestion during prolonged exercise exerts profound effects on the  
267 regulation of substrate metabolism, typically manifesting in maintenance (or higher rates) of  
268 whole-body CHO oxidation and an accompanying reduction in fat oxidation. Such alterations  
269 in substrate selection and utilisation are likely a combination of sparing of endogenous CHO  
270 stores (notably liver glycogen), maintenance of plasma glucose concentrations and a  
271 suppression in adipose tissue lipolysis or plasma fatty acid oxidation. In this way, the rationale  
272 to consume CHO during exercise (especially across durations of 2 to 6 h) is largely based on  
273 the premise of sustaining the absolute rates of whole-body CHO oxidation that are necessary  
274 to maintain the desired exercise intensity for the required exercise duration.

### 275 **3: Factors Affecting Exogenous CHO Oxidation During Exercise**

276 In the most recent sport nutrition guidelines, the upper limit of CHO intake is cited as 90 g.h<sup>-1</sup>  
277 (from products providing multiple transportable carbohydrates), as recommended for those  
278 scenarios where exercise duration is >2.5 h (22). Interestingly, earlier guidelines also suggest  
279 CHO ingestion rates between 40 and 110 g.h<sup>-1</sup> where exercise duration is > 2 h (1). In the latter  
280 case, the authors also advise glucose-fructose blends where CHO can be delivered in the form  
281 of “sports drinks / gels”, “solid sports food (low fibre and fat)” and/or “solid food”. Regardless  
282 of dose and format, however, it is noteworthy that CHO ingestion rates do not always translate  
283 to equivalent rates of exogenous CHO oxidation. As such, if an athlete intends to oxidise 90  
284 g.h<sup>-1</sup> (i.e. 1.5 g.min<sup>-1</sup>), they should likely ingest CHO at rates of 90-120 g.h<sup>-1</sup> owing to the fact  
285 that oxidation efficiency is not uniform (23, 24). Accordingly, this section offers a  
286 contemporary review of the integrated factors that can affect absolute rates of exogenous CHO  
287 oxidation during exercise, all of which are key considerations when formulating CHO feeding  
288 strategies for athletes.

289

#### 290 **3.1 Composition of CHO blends**

291 Exogenous CHO oxidation rates with glucose or glucose polymer (maltodextrin) ingestion  
292 increase in a dose-dependent manner and plateau at peak rates ranging from 0.5 to 1.1 g.min<sup>-1</sup>  
293 when ingested at rates  $\geq 1.0$ -1.2 g.min<sup>-1</sup> (52, 57). Dose-response studies have not been  
294 conducted with the other two dietary monosaccharides, fructose and galactose, but their  
295 oxidation in comparator studies feeding moderate CHO intakes (i.e., 0.65-1.2 g.min<sup>-1</sup>) is  
296 typically 25% and 50-60% lower than of glucose, respectively, (58-60), likely due, in part, to  
297 the slower intestinal absorption of fructose (61) and/or the necessity for the conversion of  
298 fructose to glucose in the liver before oxidation (62, 63). Thus, at CHO intakes up to 1 g.min<sup>-1</sup>

299 <sup>1</sup> (60 g.h<sup>-1</sup>), single source CHO (i.e., glucose or glucose polymer) is typically recommended. It  
300 should be acknowledged, however, that *blends* of glucose and fructose (including as sucrose)  
301 or glucose and galactose (including as lactose) may be equally available as oxidisable  
302 substrates at such ingestion rates, especially during prolonged sub-maximal exercise in the  
303 moderate intensity domain. For example, Hulston, et al. (64) reported comparable rates of  
304 whole-body (~2.1 g.min<sup>-1</sup>) and exogenous CHO oxidation (~0.55 g.min<sup>-1</sup>) in trained male  
305 cyclists during 2.5 h of cycling (65% VO<sub>2peak</sub>) when ingesting 0.8 g.min<sup>-1</sup> of glucose or 0.54  
306 g.min<sup>-1</sup> glucose plus 0.26 g.min<sup>-1</sup> fructose, respectively. As discussed previously (65) such data  
307 suggest glucose-fructose blends may also be applicable (or glucose polymer) even at these  
308 moderate ingestion rates due to the additional flexibility afforded if CHO intakes need to be  
309 increased as exercise progresses during a prolonged endurance event. It is noteworthy,  
310 however, that consumption of a glucose and fructose blend (in gel format) at a rate of 60 g.h<sup>-1</sup>  
311 (40 g glucose + 20 g fructose) also reduced whole-body rates of CHO oxidation by ~0.4 g.min<sup>-1</sup>  
312 <sup>1</sup> during half-marathon running (1 h 50 min) when compared with 60 g.h<sup>-1</sup> of glucose only (66).  
313 Although exogenous CHO oxidation was not quantified by these researchers, these data  
314 suggest that where there is the requirement to maintain high rates of whole-body CHO  
315 oxidation over shorter durations of higher exercise intensities (e.g. 1-2 h of exercise completed  
316 in the heavy and severe intensity domains), it may be more advisable to focus on glucose and/or  
317 maltodextrin as the predominant source of CHO. Future studies are required to directly test  
318 this hypothesis.

319         Glucose-fructose blends offer clear advantages over glucose (or glucose polymer) when  
320 ingested at high ingestion rates (e.g., up to 90 g.h<sup>-1</sup> as per current recommendations; (22)  
321 because the two monosaccharides utilise distinct intestinal luminal transporters, thereby  
322 enhancing CHO absorption and systemic carbohydrate availability during exercise (67).  
323 Countless studies have demonstrated so-called multiple transportable CHO blends to increase

324 exogenous CHO oxidation during exercise by 20-55% as compared to when an isoenergetic  
325 amount of CHO that uses a single intestinal transporter is ingested (68). Part of the high total  
326 and exogenous CHO oxidation observed with multiple transportable CHO ingestion can be  
327 attributed to fructose conversion to lactate, which is subsequently oxidised (69), hence the  
328 associated rise in blood lactate should not be misinterpreted to indicate a changing exercise  
329 intensity domain.

330 Some studies feeding multiple transportable CHO blends at very high ingestion rates  
331 (i.e., 2.0-2.4 g.min<sup>-1</sup>, 120-144 g.h<sup>-1</sup>) have observed concomitantly high average peak exogenous  
332 CHO oxidation rates (1.60-1.75 g.min<sup>-1</sup>, 96 – 105 g.h<sup>-1</sup>) (19, 23, 24). It is clear therefore that  
333 increasing CHO intakes above the currently recommended maxima of 90 g.h<sup>-1</sup> can substantially  
334 increase exogenous CHO oxidation during exercise. Also clear is that some athletes can self-  
335 select and tolerate consumption of CHO at doses greater than 90 g.h<sup>-1</sup> in certain competitive  
336 situations. Whether very high CHO intakes (i.e., above 90 g.h<sup>-1</sup>) can further enhance  
337 performance beyond that possible within existing frameworks (i.e., 60-90 g.h<sup>-1</sup> for exercise  
338 lasting over 2.5 h duration) remains to be determined.

339

### 340 **3.2. Ratio of fructose-to-glucose**

341 Since glucose and fructose can interact with one another with respect to absorption and  
342 metabolism (70, 71), the dose of each monosaccharide within a mixture may have an influence  
343 on exogenous CHO oxidation rates. To date, there have been few studies that have directly  
344 compared different ratios of glucose (polymers)-to-fructose on exogenous CHO oxidation rates  
345 and performance (see Figure 2). Of the three studies that have directly compared differing  
346 ratios, there is a consistent pattern that increasing the fructose-to-glucose ratio from ~0.4-0.5  
347 to ~0.6-1.0 results in a higher exogenous CHO oxidation rate across a range of total CHO

348 intakes spanning  $\sim 70$ - $110$  g.h<sup>-1</sup> (21, 72, 73). Furthermore, the ratio that achieved the highest  
349 exogenous CHO oxidation also resulted in the greatest improvement in exercise performance  
350 (73), supporting the concept that increasing exogenous CHO availability and oxidation, while  
351 mitigating gut discomfort can enhance exercise performance. Further work is needed to  
352 understand whether there are other factors that dictate the optimal mix of carbohydrates to  
353 ingest during exercise, but at present, it seems that a ratio of fructose-to-glucose that is between  
354 0.6-1.0 provides optimal exogenous CHO availability and oxidation.

355

### 356 **3.3. Format of CHO ingestion**

357 Although the majority of CHO feeding studies have utilised fluids (i.e. drinks) as the format of  
358 ingestion, it is noteworthy that endurance athletes commonly consume CHO in a variety of  
359 forms, including drinks, semi-solids (energy gels), and solids (energy bars, jelly chews) during  
360 both training (74) and competition (75). In support of this approach, independent laboratories  
361 (23, 76) have observed comparable exogenous CHO oxidation rates when ingesting fluids,  
362 gels, or chews (at rates of  $108$ – $120$  g.h<sup>-1</sup>) during prolonged endurance cycling. Furthermore,  
363 ingesting a mixture of these formats (as reflective of the real-world fuelling practices of  
364 endurance athletes) produces oxidation rates equivalent to each format in isolation (23).  
365 Importantly, whether consumed in isolation or co-ingested together, these formats can achieve  
366 high rates of oxidation ( $> 1.5$  g.min<sup>-1</sup>) with minimal GI distress, even at ingestion rates of up  
367 to  $120$  g.h<sup>-1</sup>. In contrast, lower exogenous CHO oxidation rates have been observed during the  
368 latter stages of prolonged endurance exercise when ingested in the form of a solid energy bar  
369 compared with a drink at ingestion rates of  $93$  g.h<sup>-1</sup> (77). Solid CHO sources are also associated  
370 with increased subjective GI symptoms (77, 78) and may be explained by delayed gastric  
371 emptying caused by the addition of protein, fat and fibre within bar formats. Taken together,  
372 the reduced rates of oxidation and increased GI distress may contribute to the decline in

373 performance observed with bar ingestion (78). However, co-ingesting solid CHO sources with  
374 other formats such as drinks and gels appears to abolish any increased GI distress and  
375 performance decline observed with bar ingestion in isolation. As such, athletes are advised to  
376 adopt a mixed-format approach using a combination of fluids, gels, jelly chews and solids,  
377 providing them with the flexibility to select formats according to individual preference, overall  
378 CHO requirements and race conditions or logistics. From a practical perspective, it should be  
379 recognised that CHO gels may be more prone to partial consumption (i.e. leftover product in  
380 the gel foil) and indirectly lead to lower ingestion rates (79), further supporting the  
381 recommendation for a mixed-format approach.

382

### 383 ***3.4 Sex specific considerations***

384 There is increased appreciation that much of what we know about sports nutrition does not  
385 adequately address the potential for sex-specific considerations, with the area of CHO feeding  
386 during exercise no exception (80). A limited number of studies have directly compared  
387 exogenous carbohydrate oxidation during exercise in men and women. Two studies have not  
388 observed clear differences between men and women with respect to absolute peak exogenous  
389 CHO oxidation rates during exercise (i.e.,  $<0.1 \text{ g}\cdot\text{min}^{-1}$  lower in women and not statistically  
390 different from men; (81, 82). In contrast, three studies provide evidence of, or the potential for,  
391 higher absolute exogenous CHO oxidation rates in men versus women, with men displaying  
392  $\sim 0.2\text{-}0.3 \text{ g}\cdot\text{min}^{-1}$  higher rates (83-85). The reason for contrasting results is likely to be multi-  
393 factorial including study design features but perhaps most critically limited statistical power to  
394 draw firm conclusions. Indeed, all the studies compared a small number of each sex, typically  
395 between 6 and 8 men or women. Larger studies are needed to clarify if there are sex-differences  
396 in absolute exogenous CHO oxidation during exercise.

397           Alternatively, if we consider metabolic responses to CHO feeding in women per se,  
398 women exhibit increased exogenous glucose oxidation as ingested glucose dose is increased  
399 up to  $60 \text{ g}\cdot\text{h}^{-1}$ , with no further increase in oxidation with glucose ingestion at  $90 \text{ g}\cdot\text{h}^{-1}$  (52). In  
400 one study, exogenous glucose oxidation was reported to not differ between women using oral  
401 triphasic hormonal contraceptives as compared to non-contraceptive users (85). Furthermore,  
402 women appear able to achieve high oxidation rates ( $\sim 1.2 \text{ g}\cdot\text{min}^{-1}$ ,  $72 \text{ g}\cdot\text{h}^{-1}$ ) with the ingestion  
403 of large amounts of multiple-transportable carbohydrates during exercise ( $2.2 \text{ g}\cdot\text{min}^{-1}$ ,  $132 \text{ g}\cdot\text{h}^{-1}$ ;  
404 (84), though such doses when ingested in males are typically associated with larger rates of  
405 exogenous CHO oxidation and greater oxidation efficiency. That said, potential sex-differences  
406 aside, there does not appear to be any inherent limitation in the capacity to utilise ingested  
407 carbohydrates for energy during exercise, and indeed the ergogenic benefit of this practice is  
408 well-established (86). Nonetheless, there is still a need to further investigate factors such as  
409 CHO dose and blend and effects of menstrual cycle and/or contraceptive use status on  
410 exogenous CHO oxidation in women. Additionally, considering the overall demand for  
411 carbohydrates in women in different contexts would ensure that female athletes can benefit  
412 from evidence-based research specific to their sex.

413

### 414 **3.5. Environmental considerations**

415 Athletes are increasingly exposed to extreme environments such as heat and hypoxia both  
416 during training and competition. Both contribute to increased metabolic perturbations during  
417 exercise and can affect whole-body metabolism by raising relative exercise intensity at a given  
418 absolute power output thereby increasing the reliance on CHO as a fuel source (87-91). At high  
419 altitude (i.e.,  $>4000 \text{ m}$ ) the ability to oxidise exogenous carbohydrates is markedly reduced  
420 (i.e., by  $\sim 20\text{-}50\%$ ) at both relative and absolute exercise intensities (92-94). Mechanistically,  
421 acute hypoxia suppresses both the systemic appearance of ingested carbohydrates and, more

422 prominently, reduces whole-body glucose disposal/metabolic clearance during exercise,  
423 alongside higher circulating glucose and insulin concentrations (92). Interestingly, this  
424 limitation appears reversible, as 3-week altitude acclimation partially restores the capacity to  
425 oxidise ingested carbohydrates (93). In practical terms, reductions in exogenous CHO  
426 oxidation rates are likely dependent on the magnitude of hypoxic stress, with existing studies  
427 typically conducted at high altitudes with large hypoxic stress that exceed those commonly  
428 experienced by most Olympic and endurance athletes both when training and racing.  
429 Furthermore, in many competitive contexts such as cycling or mountain running, exposure to  
430 altitude is transient, reducing the likelihood of meaningful metabolic impairment for the  
431 duration of the whole race. Therefore, while altitude acclimation remains advisable to optimise  
432 performance (95), there is no evidence that current CHO intake recommendations at altitude  
433 should differ from those applied at sea level.

434 Similarly, exercising in the heat at a fixed absolute workload can increase CHO  
435 demands through elevated glycogenolysis (96-98), an effect that is partially alleviated with  
436 heat acclimation (96, 99). Exogenous CHO oxidation rates, however, are consistently reduced  
437 during exercise in the heat (98, 100) by 20-30%, even when dehydration is prevented (101).  
438 Despite reductions in exogenous CHO oxidation with heat stress, high CHO availability (i.e.,  
439 before, during, and after exercise) remains important for sustaining performance in the heat, as  
440 supported by evidence that a higher-CHO diet during short-term heat acclimation improves  
441 subsequent time-trial performance in hot conditions (102). The underlying mechanisms for  
442 reductions in exogenous CHO oxidation rates are presently not fully understood but may  
443 involve slowed gastric emptying, reduced intestinal absorption due to redistribution of blood  
444 flow away from the gut, increased muscle temperature leading to accelerated glycogen  
445 breakdown, and reduced muscle glucose uptake. From a practical perspective, it is important  
446 for athletes to acclimatise to the heat, as this confers numerous thermoregulatory and

447 cardiovascular benefits (90), although evidence is lacking on effects of heat acclimation on  
448 exogenous CHO oxidation. While a reduction in exogenous CHO oxidation rates is  
449 consistently observed, the mechanisms responsible remain unclear; therefore, CHO intake  
450 recommendations should remain comparable to those used in temperate conditions.  
451 Nonetheless, a modest reduction in intake may be warranted in individuals experiencing  
452 gastrointestinal discomfort which are more likely to occur in the heat, as discussed in the  
453 following section.

454 In contrast, evidence on substrate use during exercise in cold environments is mixed,  
455 with some studies reporting reduced CHO and increased fat oxidation (103), while others,  
456 particularly those combining cold and rain exposure, have demonstrated increased CHO  
457 utilisation (104, 105). Despite these discrepancies in endogenous substrate use, exogenous  
458 CHO oxidation rates appear to be unaffected by cold exposure (106), with values comparable  
459 to those observed under thermoneutral conditions (84). Consequently, current CHO intake  
460 recommendations should remain unchanged when exercising in the cold, especially  
461 considering that maintaining blood glucose availability is especially important in these  
462 conditions, as adequate carbohydrate supply supports thermoregulatory heat production and  
463 helps prevent reductions in core temperature (107).

464

### 465 ***3.6. Gastrointestinal considerations***

466 The gastrointestinal (GI) tract determines the availability of ingested CHO during exercise  
467 through the processes of gastric emptying, intestinal transport and absorption, and subsequent  
468 delivery to the portal circulation. Strenuous or prolonged exercise challenges these processes  
469 via splanchnic hypoperfusion and heightened sympathetic activation, compromising epithelial  
470 integrity, tight-junction regulation, motility, and absorptive capacity (108). Gastrointestinal

471 symptoms are reported by a high proportion of endurance athletes across a range of sports (109-  
472 111), with potential causes being multifactorial, including circulatory (ischaemia and increased  
473 permeability), mechanical (repetitive impact), and nutritional factors including CHO dose,  
474 composition, and osmolality (112, 113). Understanding how these stressors interact with CHO  
475 feeding is therefore important to optimising fuelling strategies while minimising GI  
476 compromise.

477       Exercise-induced compromise of intestinal integrity has been linked to the onset of GI  
478 symptoms (114) and, in extreme cases, medical complications (115, 116). However, CHO  
479 ingestion during exercise has been shown to reduce markers of intestinal permeability  
480 compared with water ingestion, suggesting that exogenous substrate delivery may partially  
481 preserve epithelial integrity and limit barrier dysfunction under physiological stress (117-119).  
482 While moderate CHO ingestion may help preserve GI integrity, excessive or poorly tolerated  
483 intakes can have the negative effects of malabsorption and symptom development. When  
484 intestinal transport capacity (e.g., SGLT1 and GLUT5) is exceeded, unabsorbed  
485 glucose/fructose can potentially raise small-intestinal water content and fermentation,  
486 provoking distension and GI symptoms (120). Such GI symptoms linked to CHO intake is a  
487 potential cause for many athletes failing to meet the recommended intake during training and  
488 races.

489       A strategy to mitigate exercise-associated gastrointestinal symptoms and improve  
490 tolerance to high CHO intakes is the structured and repetitive exposure of the gut to CHO  
491 feedings, often referred to as “gut training”. Across the eight interventions included in the most  
492 recent systematic review (121), research protocols involving CHO ingestion during exercise  
493 (30-90 g·h<sup>-1</sup>) consistently reduced gut discomfort. These adaptations occurred without  
494 measurable changes in gastric emptying rate (122) or epithelial injury markers (123). While  
495 there has so far been no evidence for increases in exogenous CHO oxidation, lowered indices

496 of CHO malabsorption (assessed by post-exercise breath hydrogen) (124, 125) indicates that  
497 improvements may reflect enhanced transporter activity (e.g. SGLT1, GLUT5) and reduced  
498 sensory feedback from luminal CHO accumulation. Such adaptations are also likely reflective  
499 of daily dietary intakes as increases in exogenous CHO oxidation during exercise have been  
500 shown in athletes following a high CHO diet (8.5 g.kg.day<sup>-1</sup>) compared to a control group (5  
501 g.kg.day<sup>-1</sup>) (126). Practically, progressive exposure to higher CHO intakes during training and  
502 high dietary CHO intakes in the days and weeks prior to competition likely improves tolerance  
503 and reduces the incidence and severity of GI symptoms.

504

### 505 **3.7 CHO personalisation**

506 Current CHO intake guidelines adopt a “one-size fits all” dosing approach, as it has long been  
507 assumed that inter-individual variation in exogenous CHO oxidation is insignificant and cannot  
508 be explained by factors such as body size or metabolic rate (68). More recently, however,  
509 substantial inter-individual variability in the capacity to oxidise ingested CHO during exercise  
510 was reported (23, 127, 128). A recent study directly tested the relationship between body size  
511 and exogenous glucose oxidation by comparing smaller (<70 kg) and larger (>70 kg) trained  
512 cyclists ingesting 90 g·h<sup>-1</sup> of <sup>13</sup>C-labelled glucose during prolonged exercise (127). Larger  
513 athletes oxidised substantially more exogenous glucose (mean ~45 vs ~33 g·h<sup>-1</sup>; mean  
514 difference ~13 g·h<sup>-1</sup>) and measures of body size (mass, height, calculated body surface area)  
515 correlated strongly with peak exogenous oxidation, indicating body size is indeed a  
516 determinant factor of exogenous glucose oxidation, although it does not explain all the inter-  
517 individual variability. Importantly, when larger athletes reduced intensity to match the absolute  
518 workload of smaller athletes the difference slightly attenuated but did not disappear, implying  
519 that both body size and absolute power can contribute to the observed effect, as had been  
520 speculated previously (129).

521 Podlogar, et al. (128) recently tested whether direct measurement of an individual's  
522 peak exogenous glucose oxidation could be used to prescribe a personalised glucose dose that  
523 delivers comparable oxidation while reducing total intake. In their proof-of-concept protocol,  
524 endurance-trained participants completed two 150-min steady-state cycling trials at ~95% of  
525 LT1. In the first trial participants consumed a high glucose dose ( $90 \text{ g}\cdot\text{h}^{-1}$ ) enriched with  $^{13}\text{C}$   
526 to determine each participant's peak exogenous glucose oxidation rates. This value was then  
527 used to calculate a personalised glucose dose based on an assumed oxidation efficiency  
528 (~80%), which was given in the second trial. The personalised dose averaged  $65 \pm 10 \text{ g}\cdot\text{h}^{-1}$   
529 (~28% less than  $90 \text{ g}\cdot\text{h}^{-1}$ ) yet produced indistinguishable peak exogenous glucose oxidation  
530 rates compared with the high dose. The protocol required prolonged exercise (i.e., 2.5 h) at a  
531 sustainable steady-state intensity so that exogenous glucose oxidation rates could rise and reach  
532 a peak, which only occurs after ~2 hours of exercise (23, 24, 57, 128, 130).

533 This personalisation work focused only on the glucose-based component of CHO  
534 ingestion, typically provided as glucose polymers such as maltodextrin, representing just one  
535 component of most sports nutrition products, which usually contain both glucose- and fructose-  
536 derived carbohydrates. Because glucose and fructose use different intestinal transporters, an  
537 athlete's peak oxidation rate for one CHO type (e.g., glucose) may not predict their peak for  
538 the other (e.g., fructose). Although a 1:0.8 glucose–fructose ratio appears to approximate the  
539 average combined oxidation capacity of both substrates, inter-individual variation likely exists  
540 in the relative contribution of each, meaning that some athletes may benefit from slightly  
541 different proportions. Moreover,  $^{13}\text{C}$  co-labelling of both monosaccharides in a single test  
542 would not allow separation of their respective oxidation rates, making glucose-only testing the  
543 most pragmatic first step. In principle,  $^{14}\text{C}$  tracers could be used to distinguish both substrates  
544 simultaneously (73), but because these are radioactive, their use in human exercise studies is  
545 not ethically or practically acceptable.

546 In applied practice, personalisation offers a promising approach to maximise exogenous  
547 CHO availability without exceeding an individual's absorptive or oxidative capacity and  
548 thereby reducing the risk of gastrointestinal discomfort or unnecessary stimulation of  
549 endogenous glycogen use (20, 45, 52). Although current work demonstrates the feasibility of  
550 personalised dosing for glucose and its polymers, further research is required to understand  
551 individual variability in glucose–fructose utilisation and to determine whether similar  
552 approaches can be applied to shorter-duration exercise, where exogenous oxidation may not  
553 reach a plateau. Some athletes may be capable of tolerating and oxidising higher CHO doses  
554 than present guidelines suggest (e.g.  $>120 \text{ g}\cdot\text{h}^{-1}$ ), but identifying such individuals requires an  
555 individualised approach.

556

#### 557 **4: Contemporary Insights from Sport-Specific Research and Applied Practice**

558 The practical application of CHO feeding strategies for endurance athletes should recognise  
559 that specific endurance sports have different physiological and metabolic demands as well as  
560 practical and logistical constraints associated with CHO consumption during exercise e.g.  
561 access, format and frequency of opportunity to feed during exercise. Accordingly, this section  
562 presents a review of contemporary research findings aligned to cycling, marathon running and  
563 ultra-endurance exercise but also shares some personal reflections, insights and observations  
564 from our work as practitioners across these sports. It is noteworthy, that whilst we are  
565 witnessing a trend for athletes to consume (and experiment with) higher rates of CHO ingestion  
566 during training and racing (i.e.  $120\text{-}200 \text{ g}\cdot\text{h}^{-1}$ ), it is also acknowledged that the efficacy of such  
567 practices is not yet substantiated by current scientific research.

568

569

570 **3.1 Cycling**

571 The ergogenic effect of CHO availability on exercise capacity (14, 34) and performance during  
572 cycling (36, 37) has long been recognised. In recent years, such research has also progressed  
573 to evaluating the effects of CHO intake on sport-specific physiological determinants of  
574 performance such as durability or fatigue resistance (131). In this context, durability can be  
575 defined as the resilience to the deterioration of physiological variables and performance  
576 capability (i.e. mean and peak power output for a given duration) during or after prolonged  
577 exercise (131). Interestingly, Clark, et al. (132) reported that CHO consumption at a rate of 60  
578  $\text{g}\cdot\text{h}^{-1}$  (albeit in non-elite endurance participants) prevented the decline in critical power (CP)  
579 that occurred after 2 h of cycling within the heavy intensity domain, an effect apparent in the  
580 absence muscle glycogen sparing. In elite and professional road cyclists performing 4 h of  
581 intermittent cycling with 100  $\text{g}\cdot\text{h}^{-1}$  CHO, Ørtenblad, et al. (133) reported ~10% and ~6%  
582 reductions in 6-min time-trial mean power and sprint peak power, respectively. Overall, fat and  
583 CHO oxidation rates during the ride were not strongly related to these decrements, although  
584 higher fat oxidation in the fourth hour was modestly associated with a larger decline in 6-min  
585 power. In addition, Spragg, et al. (134) reported that in male professional cyclists, better  
586 durability (smaller reductions in CP after a severe-intensity fatiguing protocol with ~60  $\text{g}\cdot\text{h}^{-1}$   
587 CHO) was associated with lower CHO oxidation at 200 W as well as higher gross efficiency,  
588  $\dot{V}\text{O}_{2\text{max}}$  and threshold power outputs. Such data collectively suggest that an increased capacity  
589 for fat oxidation during moderate intensity exercise (so as to spare glycogen utilisation and  
590 maintain CHO availability later in exercise) may contribute to improved durability during  
591 prolonged exercise models. Such patterns of substrate utilisation are, of course, characteristic  
592 of the metabolic adaptations associated with endurance training and indeed, provide further  
593 rationale for the application of CHO periodisation during training (135). In such instances, the  
594 aim is to stimulate metabolic adaptations that subsequently promote fat oxidation during the

595 moderate and heavy intensity domains whilst retaining the capacity for high rates of CHO  
596 oxidation during the transition from the heavy to severe domain, the latter achieved through  
597 increased CHO availability late in exercise but also the training-induced adaptations in  
598 enzymatic and mitochondrial capacity to facilitate high rates of CHO oxidation when required.

599 In recognition of the ergogenic effects of CHO, the habitual intakes of professional  
600 cyclists have often been reported as 60-90 g·h<sup>-1</sup>, as is the case for both Grand Tours (136-138)  
601 and shorter stage races (75, 139). Notably, these investigations typically report mean values  
602 that are averaged across riders and stages, thereby overlooking the potential for intra-race  
603 variation and the likely periodisation of CHO intake across stages of differing physiological  
604 demand. Indeed, in accordance with the differing stage profiles (i.e. flat, hilly, mountain,  
605 summit finish etc.) and associated variations in day-to-day stage duration (i.e. 4-7 hours) and  
606 energy expenditure (which can vary between 3000-6000 kJ per day) (140-142), contemporary  
607 approaches often involve the deliberate manipulation of both daily CHO intake and “on-bike”  
608 CHO intake, with the goal of simultaneously optimising fuelling and maintaining the desired  
609 body mass for key stages. Such nutritional periodisation formed the basis of Chris Froome’s  
610 2018 Giro d’Italia victory (see Figure 3A and B), whereby CHO intake varied from 52 to 96  
611 g·h<sup>-1</sup>, the latter occurring on the most demanding stage of the race (Stage 19; on bike energy  
612 expenditure of 6180 kJ). The public disclosure of detailed Grand Tour fuelling case studies has  
613 occurred alongside a clear increase in race intensity, with recent editions of the Tour de France  
614 and other World Tour events being among the fastest in history, both in overall average speed  
615 and in record-fast stages. This combination has likely encouraged practitioners to experiment  
616 with higher CHO intakes in the modern peloton (Figure 3C). Furthermore, recent reports  
617 indicate that a stage winner on a 2025 Tour de France stage consumed approximately 116 g·h<sup>-1</sup>  
618 CHO, and some riders are now reportedly training their gastrointestinal system to tolerate 200–  
619 220 g·h<sup>-1</sup> (25). This apparent divergence between practice and the current evidence base likely

620 reflects (i) the pursuit of marginal gains in an increasingly competitive sport and (ii) the  
621 extreme energetic demands of multi-hour stages, where higher CHO intakes may help riders  
622 better match intake to expenditure and support daily energy balance (143), even if this does not  
623 necessarily confer an immediate performance benefit. As outlined in Section 3.7, substantial  
624 inter-individual variability exists in exogenous CHO oxidation capacity; notably, recent tracer  
625 work (127) reported an individual oxidising  $\sim 90 \text{ g}\cdot\text{h}^{-1}$  of ingested glucose, implying that, when  
626 combined with fructose, some athletes may have the capacity to oxidise amounts exceeding  
627  $120 \text{ g}\cdot\text{h}^{-1}$ . It is therefore plausible that a subset of riders can absorb and oxidise CHO at rates  
628 above conventional recommendations, providing a rationale for personalised approaches to  
629 CHO intake among athletes seeking optimal CHO delivery.

630         Although the practical implementation of such high CHO intakes is facilitated by  
631 advances in sports nutrition products (23), the physiological implications for CHO absorption,  
632 oxidation, gastrointestinal comfort and performance remain to be fully characterised. Based on  
633 the dosages studied to date, a CHO intake of  $90\text{--}120 \text{ g}\cdot\text{h}^{-1}$  currently represents the most  
634 evidence-based recommendation for the upper limit of CHO intakes for the majority of athletes  
635 (23, 24), but the anecdotal practices described above and the growing focus on personalised  
636 CHO intake suggest that these guidelines will likely evolve. Moreover, because race-deciding  
637 moves often now occur earlier (e.g. with 20–50 km remaining rather than within the final 5–  
638 10 km), the requirement to sustain high power output and maintain CHO dependency is  
639 probably greater than ever. Future research should therefore employ more ecologically valid  
640 exercise protocols (144) and nutritional interventions (e.g. integrating durability assessments  
641 and evaluating higher CHO doses and formats) to refine our understanding of how CHO  
642 availability influences metabolism and performance in cycling. Additional areas of practical  
643 relevance for practitioners to consider is outlined in Table 1.

644

645 **3.2. Marathon Running**

646 In contrast to cyclists, the habitual CHO intakes of marathoners (75, 145) during competition  
647 is considerably less (e.g. reported mean intakes of approximately 35 g.h<sup>-1</sup>) and at the elite level,  
648 the predominant form of CHO delivery is fluids. Such comparably low CHO intakes may be  
649 driven by a combination of behavioural factors such as lack of knowledge of CHO guidelines  
650 (146) and challenges associated with the physical opportunity to consume CHO during the race  
651 itself, but also an increased prevalence of GI symptoms associated with running (147).  
652 Nonetheless, in considering the challenge of running the “2 hour” marathon, recent modelling  
653 data has suggested the current  $\leq 90$  g.h<sup>-1</sup> recommendations would be insufficient for 65% of  
654 the modelled runners (148).

655 Indeed, although both the half-marathon (149) and marathon (150) distances are  
656 considered as CHO dependent events, recent data from the first author’s laboratory has  
657 demonstrated that CHO dependency is only maintained with higher ingestion rates of 120 g.h<sup>-1</sup>  
658 <sup>1</sup> (35). In this regard, Ravikanti, et al. (35) evaluated whole-body CHO and fat oxidation,  
659 exogenous CHO oxidation, and running economy in a cohort of male elite marathoners (all  
660 marathon PB faster than 2 h 30 minutes) while ingesting 60 (maltodextrin only), 90 (2:1  
661 maltodextrin-fructose) or 120 g.h<sup>-1</sup> (1:1 maltodextrin-fructose). The authors reported a dose  
662 dependent effect of CHO intake on whole-body and exogenous CHO oxidation and a 3%  
663 improvement in running economy with 120 g.h<sup>-1</sup> compared with the 60 g.h<sup>-1</sup> trial (see Figure  
664 4). Nonetheless, moderate symptoms of GI discomfort were reported with all doses of CHO,  
665 and peak symptoms for nausea, stomach fullness and abdominal cramps were greatest in the  
666 120 g.h<sup>-1</sup> trial. When taken together, such data demonstrate a metabolic advantage of CHO  
667 consumption at doses of 90-120 g.h<sup>-1</sup>, though the effects of such higher ingestion rates on  
668 marathon performance (in both males and females) remain to be determined, especially in  
669 consideration of the associated gastrointestinal symptoms.

670 From a practical perspective, the pattern and frequency of CHO intake during the  
671 marathon often occurs at set distance intervals (e.g. every 5 km, typically corresponding to 15  
672 min intervals) where each athlete will have their personalised fuelling options available for  
673 collection. Accordingly, the attainment of the chosen fuelling targets in-race is likely dependent  
674 on a personalised fuelling plan that has been trialled and tested in prior races and at comparable  
675 intensities and durations in training. It is noteworthy, however, that there is already a trend for  
676 marathoners to ingest higher absolute CHO doses during racing (i.e.  $> 90 \text{ g}\cdot\text{h}^{-1}$ , usually from  
677 concentrated drinks), undoubtedly due to both developments in research but also insights from  
678 elite athlete practice e.g. Eluid Kipchoge publicly disclosed racing with  $60\text{-}100 \text{ g}\cdot\text{h}^{-1}$  for the  
679 Nike Breaking 2 and the INEOS 159 project. Nonetheless, further research is required to  
680 evaluate the optimal dose, CHO ratio, frequency and format of CHO delivery (i.e. fluids versus  
681 gels) that is ergogenic for male and female runners.

682

### 683 ***3.3. Ultra-Endurance and multisport events***

684 Ultra-endurance and multisport events place substantial metabolic and gastrointestinal  
685 demands on the athlete, but they can differ markedly in the constraints they impose on fuelling.  
686 Ultra-endurance events (e.g., mountain and road ultramarathons, multiday races) can involve  
687 extreme durations and limited access to food and fluids, whereas multisport events (e.g.,  
688 triathlon/duathlon) span a wide range of race durations (from Olympic-distance to long-course)  
689 and introduce discipline-specific feeding restrictions (e.g., no intake during the swim, variable  
690 feasibility during transitions and running). Collectively, these factors create large inter- and  
691 intra-event variation in CHO intake opportunities and tolerance, and therefore in the amount  
692 and pattern of CHO that can be consumed during competition (151, 152). These constraints  
693 also determine whether athletes rely primarily on ‘collected’ fuels (e.g., frequent aid-station

694 access) or must ‘carry’ substantial CHO supplies (as is common in mountain ultramarathons  
695 and multiday events), thereby influencing both the quantity and consistency of CHO intake.

696 Evidence informing nutrition strategies in multisport events remains limited, and  
697 current guidelines are largely extrapolated from single-sport data and applied practice.  
698 Triathlon presents additional discipline-specific constraints on fuelling. During the swim,  
699 feeding is typically not feasible; therefore, pre-race CHO availability and early intake on the  
700 bike may be particularly important for whole-race CHO provision. The cycling leg generally  
701 provides the best opportunity to deliver high CHO and fluid intakes, whereas gastrointestinal  
702 symptoms are common in long-course events and may become more problematic during the  
703 run (153, 154). This occurs despite evidence that exogenous CHO oxidation rates are similar  
704 between prolonged running and cycling at comparable relative intensities (155), suggesting  
705 that discipline-specific differences in realised intake during triathlon events are driven  
706 primarily by practical constraints on ingestion while running and GI tolerance (rather than  
707 oxidation capacity *per se*). In athletes prone to GI symptoms, a pragmatic strategy may be to  
708 front-load CHO intake on the bike and modestly reduce intake late in the bike and/or early in  
709 the run to minimise symptom risk, although this approach is speculative and should be  
710 individualised. In long-course triathlon, the run is initiated after several hours of preceding  
711 exercise, and accumulated physiological strain (e.g., progressive dehydration and  
712 thermoregulatory/cardiovascular stress) may further exacerbate GI discomfort; dehydration  
713 has also been shown to impair gastric emptying and increase GI complaints during running  
714 (156). Moreover, heat stress and dehydration can influence carbohydrate metabolism during  
715 prolonged exercise (e.g., whole-body CHO oxidation and glycogen use), although direct  
716 mechanistic evidence in multisport settings remains limited and warrants further investigation  
717 (157).

718           Although the relative exercise intensity of ultra endurance exercise is lower than that  
719 of shorter endurance races (158-160), the absolute CHO cost associated with the metabolic  
720 demands of such prolonged durations have not been well characterised, particularly in elite  
721 athletes. Nonetheless, case-study observations have provided some insight to the CHO  
722 requirements to compete in such events. For example, mean whole-body CHO oxidation in a  
723 well-trained male athlete during the first 64.5 km of a 160 km mountain trail ultramarathon  
724 was  $\sim 2.1 \text{ g}\cdot\text{min}^{-1}$ , equivalent to 68% total energy expenditure (161). In a world champion male  
725 100 km runner, exercise intensity was estimated to be 74%  $\text{VO}_{2\text{max}}$  for  $\sim 6.5$  hours, with a mean  
726 whole-body CHO oxidation of  $1.6\text{-}2.3 \text{ g}\cdot\text{min}^{-1}$ , providing 68-83% of total energy expenditure  
727 throughout the race (162). In a simulated long duration triathlon, mean whole-body CHO  
728 oxidation in a male world-class triathlete was  $4.1 \text{ g}\cdot\text{min}^{-1}$  during 4 hours of cycling, but reduced  
729 to  $2.3 \text{ g}\cdot\text{min}^{-1}$  during 135 minutes of subsequent running with  $\sim 55\%$  of total energy being  
730 derived from fat oxidation (163). Sustaining whole-body CHO oxidation rates in this case study  
731 would be possible with maximal pre-exercise muscle glycogen and very high CHO  
732 consumption during exercise ( $144 \text{ g}\cdot\text{h}^{-1}$ ) although it has been suggested that the absolute  
733 exercise intensity could also be sustained from fat oxidation (164). Interestingly, maximal rate  
734 of fat oxidation has also been shown to be an independent predictor of ultra endurance  
735 performance (165) and evaluation of substrate metabolism in such elite case-studies provide  
736 further evidence that the ability for high rates of fat oxidation during prolonged exercise is a  
737 necessity to maintain the required rates of energy production.

738           In consideration of the extreme metabolic demands, there is an obvious requirement for  
739 CHO consumption during ultra-endurance exercise. Indeed, field studies report that higher  
740 rates of CHO consumption ( $66 \pm 27 \text{ g}\cdot\text{h}^{-1}$ ) are associated with greater likelihood of race  
741 completion compared to non-finishers ( $42 \pm 23 \text{ g}\cdot\text{h}^{-1}$ ) (166, 167) as well as improved  
742 physiological and ergogenic effects across a range of ultra endurance events e.g. more stable

743 blood glucose and faster finishing speeds in a 100-mile ultramarathon (168) and greater total  
744 distance covered during 24-h running (169). However, when the hourly CHO intakes are  
745 considered, many of these studies report values below the recommended intakes of  $90 \text{ g}\cdot\text{h}^{-1}$  of  
746 multiple-transportable carbohydrates. Furthermore, for races with mean finish times  $\sim 12\text{-}24$   
747 hours, intakes of between  $30\text{-}66 \text{ g}\cdot\text{h}^{-1}$  have been reported (166, 170-172). Such low intakes are  
748 likely due to a number of factors including the range of athletes studied (many are recreational,  
749 non-elite), race logistics, athlete knowledge, gastrointestinal symptoms, and an apparent  
750 aversion towards sweet tasting energy gels and sports drinks with longer durations due to  
751 changes in taste preferences (173-175). However, there are also case-studies of elite athletes  
752 consuming  $80\text{-}100 \text{ g}\cdot\text{h}^{-1}$  in both 100 mile (162) and 24-h (176) competitions. An average CHO  
753 intake of  $96 \text{ g}\cdot\text{h}^{-1}$  has also been reported by a world-class male athlete completing a 5-day 960  
754 km race (177).

755 In contrast to cycling and marathon running, the effects of CHO ingestion rates  $>90$   
756  $\text{g}\cdot\text{h}^{-1}$  on physiological responses, substrate metabolism and exercise performance are not well  
757 studied in either the laboratory or field settings. Nonetheless, it is noteworthy that CHO  
758 ingestion rates of  $120 \text{ g}\cdot\text{h}^{-1}$  in male elite runners during a mountain marathon reduced post-race  
759 markers of exercise-induced muscle damage (EIMD) compared to  $60$  and  $90 \text{ g}\cdot\text{h}^{-1}$  (178). Given  
760 that EIMD has been suggested to be a major determinant in ultra-endurance performance (178),  
761 this may be another mechanism for improved performance with higher CHO doses.

762 From a practical perspective, a critical success factor underpinning ultra-endurance  
763 performance depends on the ability to sustain CHO intake whilst also minimising GI symptoms  
764 under diverse and unpredictable race conditions. Indeed, the practical delivery of CHO is  
765 multifaceted in such a wide array of events and may change athlete-to-athlete, race-to-race and  
766 within sections of races. Evidence from laboratory, field, and elite case studies suggests that  
767 well-trained athletes who progressively train the gut could tolerate  $\geq 90 \text{ g}\cdot\text{h}^{-1}$  of multiple-

768 transportable CHO, implemented through personalised and adaptable fuelling plans. Indeed,  
769 there are recent anecdotal reports of athletes consuming  $>120 \text{ g}\cdot\text{h}^{-1}$  in some of the most difficult  
770 100-mile races exposed to high environmental temperatures and altitudes (179), though  
771 empirical research (in both males and females) is needed to support the efficacy of such  
772 strategies. Our reflections from supporting such athletes are that the most common  
773 determinants of whether high CHO intakes are achieved is, in fact, an initial *belief* in the  
774 importance of CHO for promoting performance, as well as race fuelling preparation, gut  
775 tolerance and logistics associated with the race itself. In addition, access to a well-coordinated  
776 crew support, innovations in delivery (such as cold or semi-frozen CHO drinks used  
777 strategically in hot environments) and the availability of well formulated and more palatable  
778 sports nutrition products can also promote in-race fuelling behaviours. Further research is  
779 required to explore the barriers and enablers to fuelling in both training and racing scenarios.

780

## 781 **5: Towards contemporary CHO guidelines for athletes**

782 The 2016 guidelines from the American College of Sports Medicine recommend CHO intakes  
783 of  $30\text{-}60 \text{ g}\cdot\text{h}^{-1}$  (for endurance exercise and “stop and start” sports lasting 1- 2.5 h) and  $90 \text{ g}\cdot\text{h}^{-1}$ ,  
784 the latter dose targeted to “ultra-endurance” exercise that is  $>2.5$  to 3 h in duration. However,  
785 in view of the recent research developments discussed within the present review, it would now  
786 seem timely to provide updated and more nuanced guidelines that also consider the interaction  
787 between the target exercise intensity and typical durations associated with specific endurance  
788 and ultra-endurance sporting scenarios (see Figure 5). In this context, we define ultra-  
789 endurance exercise as durations  $>6$  h, where exercise scenarios spanning 1-6 h are more  
790 representative of the typical durations and intensities associated with team sport activity (e.g.  
791 soccer), half-marathon, marathons and road cycling stages. Importantly, it is also suggested  
792 that the upper limit of CHO intake could increase from  $90$  to  $120 \text{ g}\cdot\text{h}^{-1}$  (at least in trained

793 participants), considering that both exogenous and whole-body rates of CHO oxidation can be  
794 increased with these higher ingestion rates (19, 23, 24).

795         Although our theoretical model to guide CHO ingestion also considers the whole-body  
796 CHO oxidation rates that are aligned to the maintenance of exercise intensity for a given  
797 duration, we readily acknowledge that the cited absolute CHO oxidation rates are reflective  
798 from investigations conducted on male athletes. Accordingly, the need to provide comparable  
799 data from female athletes is recognised as a major research priority. Furthermore, it is  
800 noteworthy that even with these higher rates of CHO ingestion, the sum of both endogenous  
801 and exogenous CHO availability is unlikely to provide all of the necessary substrate to sustain  
802 the required rates of energy production during exercise, especially as exercise duration  
803 increases beyond 2 hours. As such, we consider that the high absolute rates of fat oxidation  
804 observed in marathoners (35), cyclists and ultra-endurance athletes (163) (even at intensities  
805 associated with race pace) demonstrate that fat does not provide a negligible contribution to  
806 energy production, but rather, is indicative that fat provides an obligatory fuel source for elite  
807 endurance performance. When considered this way, training and nutritional strategies (e.g.  
808 train-low models aligned to CHO periodisation and *fuelling for the work required*) that optimise  
809 the capacity to oxidise both carbohydrate *and* fat on race day would seem a major goal for the  
810 elite endurance athlete (135)

811

## 812 **6: Summary and Directions for Future Research**

813 Despite over 100 years of scientific research, the effects of CHO intake during exercise on  
814 substrate metabolism and exercise performance continues to be at the forefront of the nutrition  
815 related performance questions posed by both the scientific and athletic community. In this  
816 regard, the apparent trend of higher CHO intakes (i.e.  $>90 \text{ g}\cdot\text{h}^{-1}$ ) in elite endurance and ultra-

817 endurance athletes is in accordance with recent research developments, at least for ingestion  
818 rates up to 120 g.h<sup>-1</sup>. Nonetheless, considerable opportunities exist to advance our  
819 understanding of the optimal dose, frequency, ratio, and format of CHO ingestion that is  
820 ergogenic to male and female athletes, especially in consideration of the potential trade-off  
821 between optimising CHO availability and any associated gastrointestinal symptoms. In  
822 addition to such specific areas of investigation that are likely to inform “CHO personalisation”  
823 strategies, there are also a number of bigger picture related themes that should be considered  
824 in future research.

825         Indeed, the translational potential of original research will only ever be as good as the  
826 relevance of the training status of the research participants, the nutritional intervention and the  
827 validity of the exercise protocol to the situation of the intended end-user (180). In the context  
828 of the elite endurance athlete and CHO feeding during exercise, it is noteworthy that recent  
829 research audits have demonstrated that < 5% of research studies have been conducted on tier 4  
830 (elite / international) and tier 5 athletes (world class) (181), as categorised according to the  
831 Participant Classification Framework (182). As such, our current understanding of CHO  
832 feeding during exercise is largely based on studies (>80%) conducted on tier 1 (recreationally  
833 active) and tier 2 (trained / developmental) participants, of which the pattern of substrate  
834 utilisation during exercise (especially the capacity for high absolute rates of fat oxidation) is  
835 likely to be very different than elite athletes (see Figure 6). The requirement to study female  
836 participants (across all tiers of classification) is a clear research priority, especially when  
837 considering that <3% of studies have adopted female only cohorts (80). Accordingly, there is a  
838 definitive need to further characterise the habitual fuelling practices and substrate metabolism  
839 of elite endurance and ultra-endurance male and female athletes during both training and  
840 competition, the result of which should allow researchers to better design both laboratory and  
841 field-based studies (e.g. (30) that evaluate the effects of CHO feeding strategies in conditions

842 that are more applicable to real world contexts. Furthermore, the mechanism(s) by which acute  
843 environmental stressors (e.g. heat and/or hyoxia) reduces exogenous CHO oxidation rates (and  
844 also remain to be determined, as does the potential for relevant acclimatisation strategies to  
845 reverse such decrements.

846 In considering the difficulties associated with assessing outcome measures of  
847 competitive performance (i.e. reliable and valid testing protocols), such studies should also  
848 assess the effects of CHO availability on the underlying physiological determinants of  
849 performance that are of relevance to the specific sporting scenario e.g. economy, efficiency,  
850 durability, resilience etc. Finally, when considering the necessity for high absolute rates of fat  
851 oxidation to sustain the required rates of energy production (even in the presence of high CHO  
852 availability), the interaction of training and nutritional strategies aligned to optimising the  
853 capacity for both CHO (e.g. gut training protocols) and fat oxidation (e.g. models of train-low  
854 and CHO periodisation) is also considered an important area for future research. When taken  
855 together, it is clear that such a fundamental component of sports nutrition research and practice  
856 remains as exciting as ever, and it is hoped that this paper will stimulate collaborative efforts  
857 worldwide between scientists, athletes, coaches, and practitioners to further develop the  
858 personalisation of CHO guidelines for athletes.

#### 859 **Statement of authors' contributions to manuscript**

860 JPM conceived the initial content and structure of the review with primary responsibility for  
861 final content. JPM, JMF, JTG, MAH, TP, JNP and GAW all contributed to the writing of this  
862 manuscript. Figures were prepared by JPM, JTG, JMF and MAH. All authors have read and  
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865

#### 866 **Conflicts of interest**

867 JPM is a consultant for Science in Sport Ltd (SiS) and former employee of Team Sky (Tour  
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 873 Fruit Juice Science Centre; is a scientific advisory board member to ZOE; and has completed  
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### 885 **References**

886

- 887 1. Stellingwerff T, Cox GR. Systematic review: Carbohydrate supplementation on  
 888 exercise performance or capacity of varying durations. *Appl Physiol Nutr Metab.*  
 889 2014;39(9):998-1011. doi: 10.1139/apnm-2014-0027.
- 890 2. Levine SA, Gordon B, Derick CL. Some changes in the chemical constituents of the  
 891 blood following a marathon race: with special reference to the development of  
 892 hypoglycemia. *Journal of the American Medical Association.* 1924;82(22):1778-9. doi:  
 893 10.1001/jama.1924.02650480034015.
- 894 3. Gordon B, Kohn LA, Levine SA, Matton M, Scriver WdM, Whiting WB. Sugar content  
 895 of the blood in runners following a marathon race with especial reference to the  
 896 prevention of hypoglycemia: further observations. *Journal of the American Medical*  
 897 *Association.* 1925;85(7):508-9. doi: 10.1001/jama.1925.02670070028009.
- 898 4. Bergström J, Hermansen L, Hultman E, Saltin B. Diet, muscle glycogen and physical  
 899 performance. *Acta Physiol Scand.* 1967;71(2):140-50. doi: 10.1111/j.1748-  
 900 1716.1967.tb03720.x.
- 901 5. Bergström J, Hultman E. The effect of exercise on muscle glycogen and electrolytes in  
 902 normals. *Scand J Clin Lab Invest.* 1966;18(1):16-20. doi:  
 903 10.3109/00365516609065602.
- 904 6. Costill DL, Gollnick PD, Jansson ED, Saltin B, Stein EM. Glycogen depletion pattern  
 905 in human muscle fibres during distance running. *Acta Physiol Scand.* 1973;89(3):374-  
 906 83. doi: 10.1111/j.1748-1716.1973.tb05532.x.

- 907 7. Gollnick PD, Armstrong RB, Saubert CWt, Sembrowich WL, Shepherd RE, Saltin B.  
908 Glycogen depletion patterns in human skeletal muscle fibers during prolonged work.  
909 *Pflugers Arch.* 1973;344(1):1-12. doi: 10.1007/bf00587437.
- 910 8. Gollnick PD, Piehl K, Saltin B. Selective glycogen depletion pattern in human muscle  
911 fibres after exercise of varying intensity and at varying pedalling rates. *J Physiol.*  
912 1974;241(1):45-57. doi: 10.1113/jphysiol.1974.sp010639.
- 913 9. Karlsson J, Nordesjö LO, Saltin B. Muscle glycogen utilization during exercise after  
914 physical training. *Acta Physiol Scand.* 1974;90(1):210-7. doi: 10.1111/j.1748-  
915 1716.1974.tb05579.x.
- 916 10. Karlsson J, Saltin B. Diet, muscle glycogen, and endurance performance. *J Appl*  
917 *Physiol.* 1971;31(2):203-6. doi: 10.1152/jappl.1971.31.2.203.
- 918 11. Coggan AR, Coyle EF. Reversal of fatigue during prolonged exercise by carbohydrate  
919 infusion or ingestion. *J Appl Physiol* (1985). 1987;63(6):2388-95. doi:  
920 10.1152/jappl.1987.63.6.2388.
- 921 12. Coggan AR, Coyle EF. Effect of carbohydrate feedings during high-intensity exercise.  
922 *J Appl Physiol* (1985). 1988;65(4):1703-9. doi: 10.1152/jappl.1988.65.4.1703.
- 923 13. Coggan AR, Coyle EF. Metabolism and performance following carbohydrate ingestion  
924 late in exercise. *Med Sci Sports Exerc.* 1989;21(1):59-65. doi: 10.1249/00005768-  
925 198902000-00011.
- 926 14. Coyle EF, Coggan AR, Hemmert MK, Ivy JL. Muscle glycogen utilization during  
927 prolonged strenuous exercise when fed carbohydrate. *J Appl Physiol* (1985).  
928 1986;61(1):165-72. doi: 10.1152/jappl.1986.61.1.165.
- 929 15. Coyle EF, Hagberg JM, Hurley BF, Martin WH, Ehsani AA, Holloszy JO. Carbohydrate  
930 feeding during prolonged strenuous exercise can delay fatigue. *J Appl Physiol Respir*  
931 *Environ Exerc Physiol.* 1983;55(1 Pt 1):230-5. doi: 10.1152/jappl.1983.55.1.230.
- 932 16. Massicotte D, Péronnet F, Allah C, Hillaire-Marcel C, Ledoux M, Brisson G. Metabolic  
933 response to [13C]glucose and [13C]fructose ingestion during exercise. *J Appl Physiol*  
934 (1985). 1986;61(3):1180-4. doi: 10.1152/jappl.1986.61.3.1180.
- 935 17. Pirnay F, Crielaard JM, Pallikarakis N, Lacroix M, Mosora F, Krzentowski G, et al.  
936 Fate of exogenous glucose during exercise of different intensities in humans. *J Appl*  
937 *Physiol Respir Environ Exerc Physiol.* 1982;53(6):1620-4. doi:  
938 10.1152/jappl.1982.53.6.1620.
- 939 18. Jeukendrup AE, Wagenmakers AJ, Stegen JH, Gijsen AP, Brouns F, Saris WH.  
940 Carbohydrate ingestion can completely suppress endogenous glucose production  
941 during exercise. *Am J Physiol.* 1999;276(4):E672-83. doi:  
942 10.1152/ajpendo.1999.276.4.E672.
- 943 19. Jentjens RL, Jeukendrup AE. High rates of exogenous carbohydrate oxidation from a  
944 mixture of glucose and fructose ingested during prolonged cycling exercise. *Br J Nutr.*  
945 2005;93(4):485-92. doi: 10.1079/bjn20041368.

- 946 20. Jentjens RL, Moseley L, Waring RH, Harding LK, Jeukendrup AE. Oxidation of  
947 combined ingestion of glucose and fructose during exercise. *J Appl Physiol* (1985).  
948 2004;96(4):1277-84. doi: 10.1152/jappphysiol.00974.2003.
- 949 21. Jentjens RL, Shaw C, Birtles T, Waring RH, Harding LK, Jeukendrup AE. Oxidation of  
950 combined ingestion of glucose and sucrose during exercise. *Metabolism*.  
951 2005;54(5):610-8.
- 952 22. Thomas DT, Erdman KA, Burke LM. American College of Sports Medicine Joint  
953 Position Statement. Nutrition and Athletic Performance. *Med Sci Sports Exerc*.  
954 2016;48(3):543-68. doi: 10.1249/mss.0000000000000852.
- 955 23. Hearris MA, Pugh JN, Langan-Evans C, Mann SJ, Burke L, Stellingwerff T, et al.  
956 (13)C-glucose-fructose labeling reveals comparable exogenous CHO oxidation during  
957 exercise when consuming 120 g/h in fluid, gel, jelly chew, or coingestion. *J Appl*  
958 *Physiol* (1985). 2022;132(6):1394-406. doi: 10.1152/jappphysiol.00091.2022.
- 959 24. Podlogar T, Bokal Š, Cirnski S, Wallis GA. Increased exogenous but unaltered  
960 endogenous carbohydrate oxidation with combined fructose-maltodextrin ingested at  
961 120 g h<sup>-1</sup> versus 90 g h<sup>-1</sup> at different ratios. *Eur J Appl Physiol*.  
962 2022;122(11):2393-401. doi: 10.1007/s00421-022-05019-w.
- 963 25. Whitehead J. 6,252 calories and 1,245 grams of carbs: What it takes to fuel a winning  
964 ride at the Tour de France. 2025.
- 965 26. van Loon LJ, Greenhaff PL, Constantin-Teodosiu D, Saris WH, Wagenmakers AJ. The  
966 effects of increasing exercise intensity on muscle fuel utilisation in humans. *J Physiol*.  
967 2001;536(Pt 1):295-304. doi: 10.1111/j.1469-7793.2001.00295.x.
- 968 27. Watt MJ, Heigenhauser GJ, Dyck DJ, Spriet LL. Intramuscular triacylglycerol,  
969 glycogen and acetyl group metabolism during 4 h of moderate exercise in man. *J*  
970 *Physiol*. 2002;541(Pt 3):969-78. doi: 10.1113/jphysiol.2002.018820.
- 971 28. Martin WH, 3rd, Dalsky GP, Hurley BF, Matthews DE, Bier DM, Hagberg JM, et al.  
972 Effect of endurance training on plasma free fatty acid turnover and oxidation during  
973 exercise. *Am J Physiol*. 1993;265(5 Pt 1):E708-14. doi:  
974 10.1152/ajpendo.1993.265.5.E708.
- 975 29. Bartlett JD, Louhelainen J, Iqbal Z, Cochran AJ, Gibala MJ, Gregson W, et al. Reduced  
976 carbohydrate availability enhances exercise-induced p53 signaling in human skeletal  
977 muscle: implications for mitochondrial biogenesis. *Am J Physiol Regul Integr Comp*  
978 *Physiol*. 2013;304(6):R450-8. doi: 10.1152/ajpregu.00498.2012.
- 979 30. Burke LM, Ross ML, Garvican-Lewis LA, Welvaert M, Heikura IA, Forbes SG, et al.  
980 Low carbohydrate, high fat diet impairs exercise economy and negates the performance  
981 benefit from intensified training in elite race walkers. *J Physiol*. 2017;595(9):2785-807.  
982 doi: 10.1113/jp273230.
- 983 31. Hargreaves M, McConell G, Proietto J. Influence of muscle glycogen on  
984 glycogenolysis and glucose uptake during exercise in humans. *J Appl Physiol* (1985).  
985 1995;78(1):288-92. doi: 10.1152/jappl.1995.78.1.288.

- 986 32. Montain SJ, Hopper MK, Coggan AR, Coyle EF. Exercise metabolism at different time  
987 intervals after a meal. *J Appl Physiol* (1985). 1991;70(2):882-8. doi:  
988 10.1152/jappl.1991.70.2.882.
- 989 33. Wee SL, Williams C, Tsintzas K, Boobis L. Ingestion of a high-glycemic index meal  
990 increases muscle glycogen storage at rest but augments its utilization during subsequent  
991 exercise. *J Appl Physiol* (1985). 2005;99(2):707-14. doi:  
992 10.1152/jappphysiol.01261.2004.
- 993 34. Fell JM, Hearn MA, Ellis DG, Moran JEP, Jevons EFP, Owens DJ, et al. Carbohydrate  
994 improves exercise capacity but does not affect subcellular lipid droplet morphology,  
995 AMPK and p53 signalling in human skeletal muscle. *J Physiol*. 2021;599(11):2823-49.  
996 doi: 10.1113/jp281127.
- 997 35. Ravikanti S, Silang KG, Martyn HJ, Johnson KO, Louis JB, Bampouras TM, et al. <sup>13</sup>C  
998 labelled glucose-fructose show greater exogenous and whole-body CHO oxidation and  
999 lower O<sub>2</sub> cost of running at 120 vs 60 & 90 g·h<sup>-1</sup> in elite male marathoners. *J Appl*  
1000 *Physiol* (1985). 2025. doi: 10.1152/jappphysiol.00665.2025.
- 1001 36. Smith JW, Zachwieja JJ, Péronnet F, Passe DH, Massicotte D, Lavoie C, et al. Fuel  
1002 selection and cycling endurance performance with ingestion of [<sup>13</sup>C]glucose: evidence  
1003 for a carbohydrate dose response. *J Appl Physiol* (1985). 2010;108(6):1520-9. doi:  
1004 10.1152/jappphysiol.91394.2008.
- 1005 37. Smith JW, Pascoe DD, Passe DH, Ruby BC, Stewart LK, Baker LB, et al. Curvilinear  
1006 dose-response relationship of carbohydrate (0-120 g·h(-1)) and performance. *Med Sci*  
1007 *Sports Exerc*. 2013;45(2):336-41. doi: 10.1249/MSS.0b013e31827205d1.
- 1008 38. Gonzalez JT, Fuchs CJ, Betts JA, van Loon LJ. Liver glycogen metabolism during and  
1009 after prolonged endurance-type exercise. *Am J Physiol Endocrinol Metab*.  
1010 2016;311:E543-53.
- 1011 39. Nuttall FQ, Ngo A, Gannon MC. Regulation of hepatic glucose production and the role  
1012 of gluconeogenesis in humans: is the rate of gluconeogenesis constant? *Diabetes Metab*  
1013 *Res Rev*. 2008;24(6):438-58. doi: 10.1002/dmrr.863.
- 1014 40. Fuchs CJ, Veeraiah P, Hermans WJH, Brauwiers B, Voncken R, Brouwers K, et al.  
1015 Carbohydrate intake of 10 g/kg body mass rapidly replenishes liver, but not muscle  
1016 glycogen contents, during 12 h of post-exercise recovery in well-trained cyclists. *J*  
1017 *Physiol*. 2025. doi: 10.1113/jp289115.
- 1018 41. Rollo I, Gonzalez JT, Fuchs CJ, van Loon LJ, Williams C. Primary, secondary, and  
1019 tertiary effects of carbohydrate ingestion during exercise. *Sports Medicine*.  
1020 2020;50:1863-71.
- 1021 42. Maughan RJ, Bethell LR, Leiper JB. Effects of ingested fluids on exercise capacity and  
1022 on cardiovascular and metabolic responses to prolonged exercise in man. *Exp Physiol*.  
1023 1996;81(5):847-59. doi: 10.1113/expphysiol.1996.sp003981.
- 1024 43. Gonzalez JT, Fuchs CJ, Smith FE, Thelwall PE, Taylor R, Stevenson EJ, et al. Ingestion  
1025 of glucose or sucrose prevents liver but not muscle glycogen depletion during

- 1026 prolonged endurance-type exercise in trained cyclists. *American Journal of Physiology-*  
1027 *Endocrinology and Metabolism*. 2015;309(12):1032-9.
- 1028 44. King AJ, O'Hara JP, Arjomandkhah NC, Rowe J, Morrison DJ, Preston T, et al. Liver  
1029 and muscle glycogen oxidation and performance with dose variation of glucose–  
1030 fructose ingestion during prolonged (3 h) exercise. *European Journal of Applied*  
1031 *Physiology*. 2019;119(5):1157-69.
- 1032 45. King AJ, O'Hara JP, Morrison DJ, Preston T, King RF. Carbohydrate dose influences  
1033 liver and muscle glycogen oxidation and performance during prolonged exercise.  
1034 *Physiological reports*. 2018;6(1):e13555.
- 1035 46. Jeukendrup AE, Moseley L, Mainwaring GI, Samuels S, Perry S, Mann CH. Exogenous  
1036 carbohydrate oxidation during ultraendurance exercise. *Journal of Applied Physiology*.  
1037 2006;100(4):1134-41.
- 1038 47. Menzies C, Wood M, Thomas J, Hengist A, Walhin J-P, Jones R, et al. Frequent  
1039 carbohydrate ingestion reduces muscle glycogen depletion and postpones fatigue  
1040 relative to a single bolus. *International journal of sport nutrition and exercise*  
1041 *metabolism*. 2020;30(3):203-9.
- 1042 48. Tsintzas OK, Williams C, Boobis L, Greenhaff P. Carbohydrate ingestion and single  
1043 muscle fiber glycogen metabolism during prolonged running in men. *J Appl Physiol*  
1044 (1985). 1996;81(2):801-9. doi: 10.1152/jappl.1996.81.2.801.
- 1045 49. Rothschild JA, Dudley-Rode H, Carpenter H, Smith ASM, Plews DJ, Maunder E.  
1046 Carbohydrate ingestion during prolonged exercise and net skeletal muscle glycogen  
1047 utilization: a meta-analysis. *J Appl Physiol* (1985). 2026;140(1):76-87. doi:  
1048 10.1152/japplphysiol.00861.2025.
- 1049 50. Kuipers H, Keizer HA, Brouns F, Saris WH. Carbohydrate feeding and glycogen  
1050 synthesis during exercise in man. *Pflugers Arch*. 1987;410(6):652-6. doi:  
1051 10.1007/bf00581327.
- 1052 51. Kuipers H, Saris W, Brouns F, Keizer H, Ten Bosch C. Glycogen synthesis during  
1053 exercise and rest with carbohydrate feeding in males and females. *International journal*  
1054 *of sports medicine*. 1989;10(S 1):S63-S7.
- 1055 52. Wallis GA, Yeo SE, Blannin AK, Jeukendrup AE. Dose-response effects of ingested  
1056 carbohydrate on exercise metabolism in women. *Med Sci Sports Exerc*.  
1057 2007;39(1):131-8. doi: 10.1249/01.mss.0000241645.28467.d3.
- 1058 53. Horowitz JF, Mora-Rodriguez R, Byerley LO, Coyle EF. Lipolytic suppression  
1059 following carbohydrate ingestion limits fat oxidation during exercise. *Am J Physiol*.  
1060 1997;273(4):E768-75. doi: 10.1152/ajpendo.1997.273.4.E768.
- 1061 54. Newell ML, Wallis GA, Hunter AM, Tipton KD, Galloway SDR. Metabolic Responses  
1062 to Carbohydrate Ingestion during Exercise: Associations between Carbohydrate Dose  
1063 and Endurance Performance. *Nutrients*. 2018;10(1). doi: 10.3390/nu10010037.

- 1064 55. Coyle EF, Jeukendrup AE, Wagenmakers AJ, Saris WH. Fatty acid oxidation is directly  
1065 regulated by carbohydrate metabolism during exercise. *Am J Physiol.* 1997;273(2 Pt  
1066 1):E268-75. doi: 10.1152/ajpendo.1997.273.2.E268.
- 1067 56. Stokie JR, Abbott G, Howlett KF, Hamilton DL, Shaw CS. Intramuscular lipid  
1068 utilization during exercise: a systematic review, meta-analysis, and meta-regression. *J  
1069 Appl Physiol (1985).* 2023;134(3):581-92. doi: 10.1152/jappphysiol.00637.2021.
- 1070 57. Jeukendrup AE, Jentjens R. Oxidation of carbohydrate feedings during prolonged  
1071 exercise: current thoughts, guidelines and directions for future research. *Sports Med.*  
1072 2000;29(6):407-24. doi: 10.2165/00007256-200029060-00004.
- 1073 58. Burelle Y, Lamoureux MC, Péronnet F, Massicotte D, Lavoie C. Comparison of  
1074 exogenous glucose, fructose and galactose oxidation during exercise using <sup>13</sup>C-  
1075 labelling. *Br J Nutr.* 2006;96(1):56-61. doi: 10.1079/bjn20061799.
- 1076 59. Leijssen DP, Saris WH, Jeukendrup AE, Wagenmakers AJ. Oxidation of exogenous  
1077 [<sup>13</sup>C]galactose and [<sup>13</sup>C]glucose during exercise. *J Appl Physiol (1985).*  
1078 1995;79(3):720-5. doi: 10.1152/jappl.1995.79.3.720.
- 1079 60. Murray R, Paul GL, Seifert JG, Eddy DE, Halaby GA. The effects of glucose, fructose,  
1080 and sucrose ingestion during exercise. *Med Sci Sports Exerc.* 1989;21(3):275-82.
- 1081 61. Ravich WJ, Bayless TM, Thomas M. Fructose: incomplete intestinal absorption in  
1082 humans. *Gastroenterology.* 1983;84(1):26-9.
- 1083 62. Jandrain BJ, Pallikarakis N, Normand S, Pirnay F, Lacroix M, Mosora F, et al. Fructose  
1084 utilization during exercise in men: rapid conversion of ingested fructose to circulating  
1085 glucose. *J Appl Physiol (1985).* 1993;74(5):2146-54. doi:  
1086 10.1152/jappl.1993.74.5.2146.
- 1087 63. Massicotte D, Péronnet F, Brisson G, Bakkouch K, Hillaire-Marcel C. Oxidation of a  
1088 glucose polymer during exercise: comparison with glucose and fructose. *J Appl Physiol  
1089 (1985).* 1989;66(1):179-83. doi: 10.1152/jappl.1989.66.1.179.
- 1090 64. Hulston CJ, Wallis GA, Jeukendrup AE. Exogenous CHO oxidation with glucose plus  
1091 fructose intake during exercise. *Med Sci Sports Exerc.* 2009;41(2):357-63. doi:  
1092 10.1249/MSS.0b013e3181857ee6.
- 1093 65. Podlogar T, Wallis GA. *New Horizons in Carbohydrate Research and Application for  
1094 Endurance Athletes.* *Sports Med.* 2022;52(Suppl 1):5-23. doi: 10.1007/s40279-022-  
1095 01757-1.
- 1096 66. Lee MJ, Hammond KM, Vasdev A, Poole KL, Impey SG, Close GL, et al. Self-selecting  
1097 fluid intake while maintaining high carbohydrate availability does not impair half-  
1098 marathon performance. *Int J Sports Med.* 2014;35(14):1216-22. doi: 10.1055/s-0034-  
1099 1375635.
- 1100 67. Rowlands DS, Houltham S, Musa-Veloso K, Brown F, Paulionis L, Bailey D. Fructose-  
1101 Glucose Composite Carbohydrates and Endurance Performance: Critical Review and  
1102 Future Perspectives. *Sports Med.* 2015;45(11):1561-76. doi: 10.1007/s40279-015-  
1103 0381-0.

- 1104 68. Jeukendrup AE. Carbohydrate and exercise performance: the role of multiple  
1105 transportable carbohydrates. *Curr Opin Clin Nutr Metab Care*. 2010;13(4):452-7. doi:  
1106 10.1097/MCO.0b013e328339de9f.
- 1107 69. Lecoultre V, Benoit R, Carrel G, Schutz Y, Millet GP, Tappy L, et al. Fructose and  
1108 glucose co-ingestion during prolonged exercise increases lactate and glucose fluxes and  
1109 oxidation compared with an equimolar intake of glucose. *Am J Clin Nutr*.  
1110 2010;92(5):1071-9. doi: 10.3945/ajcn.2010.29566.
- 1111 70. Truswell AS, Seach JM, Thorburn A. Incomplete absorption of pure fructose in healthy  
1112 subjects and the facilitating effect of glucose. *The American journal of clinical*  
1113 *nutrition*. 1988;48(6):1424-30.
- 1114 71. Petersen KF, Laurent D, Yu C, Cline GW, Shulman GI. Stimulating effects of low-dose  
1115 fructose on insulin-stimulated hepatic glycogen synthesis in humans. *Diabetes*.  
1116 2001;50(6):1263-8.
- 1117 72. O'Brien WJ, Rowlands DS. Fructose-maltodextrin ratio in a carbohydrate-electrolyte  
1118 solution differentially affects exogenous carbohydrate oxidation rate, gut comfort, and  
1119 performance. *American Journal of Physiology-Gastrointestinal and Liver Physiology*.  
1120 2011;300(1):G181-G9.
- 1121 73. O'Brien WJ, Stannard SR, Clarke JA, Rowlands DS. Fructose-maltodextrin ratio  
1122 governs exogenous and other CHO oxidation and performance. *Med Sci Sports Exerc*.  
1123 2013;45(9):1814-24. doi: 10.1249/MSS.0b013e31828e12d4.
- 1124 74. Reinhard C, Galloway SDR. Carbohydrate Intake Practices and Determinants of Food  
1125 Choices During Training in Recreational, Amateur, and Professional Endurance  
1126 Athletes: A Survey Analysis. *Front Nutr*. 2022;9:862396. doi:  
1127 10.3389/fnut.2022.862396.
- 1128 75. Pfeiffer B, Stellingwerff T, Hodgson AB, Randell R, Pöttgen K, Res P, et al. Nutritional  
1129 intake and gastrointestinal problems during competitive endurance events. *Med Sci*  
1130 *Sports Exerc*. 2012;44(2):344-51. doi: 10.1249/MSS.0b013e31822dc809.
- 1131 76. Pfeiffer B, Stellingwerff T, Zaltas E, Jeukendrup AE. CHO oxidation from a CHO gel  
1132 compared with a drink during exercise. *Med Sci Sports Exerc*. 2010;42(11):2038-45.  
1133 doi: 10.1249/MSS.0b013e3181e0efe6.
- 1134 77. Pfeiffer B, Stellingwerff T, Zaltas E, Jeukendrup AE. Oxidation of solid versus liquid  
1135 CHO sources during exercise. *Med Sci Sports Exerc*. 2010;42(11):2030-7. doi:  
1136 10.1249/MSS.0b013e3181e0efc9.
- 1137 78. Guillochon M, Rowlands DS. Solid, Gel, and Liquid Carbohydrate Format Effects on  
1138 Gut Comfort and Performance. *Int J Sport Nutr Exerc Metab*. 2017;27(3):247-54. doi:  
1139 10.1123/ijsnem.2016-0211.
- 1140 79. Lanpir AD, Eroğlu MN, Özyıldırım M, Louis J. Under Consumed and Overestimated:  
1141 Discrepancies in Race-Day Carbohydrate Intake Among Endurance Athletes. *Eur J*  
1142 *Sport Sci*. 2025;25(11):e70055. doi: 10.1002/ejsc.70055.

- 1143 80. Kuikman MA, Smith ES, McKay AKA, Ackerman KE, Harris R, Elliott-Sale KJ, et al.  
1144 Fueling the Female Athlete: Auditing Her Representation in Studies of Acute  
1145 Carbohydrate Intake for Exercise. *Med Sci Sports Exerc.* 2023;55(3):569-80. doi:  
1146 10.1249/mss.0000000000003056.
- 1147 81. Riddell MC, Partington SL, Stupka N, Armstrong D, Rennie C, Tarnopolsky MA.  
1148 Substrate utilization during exercise performed with and without glucose ingestion in  
1149 female and male endurance trained athletes. *Int J Sport Nutr Exerc Metab.*  
1150 2003;13(4):407-21. doi: 10.1123/ijsnem.13.4.407.
- 1151 82. Wallis GA, Dawson R, Achten J, Webber J, Jeukendrup AE. Metabolic response to  
1152 carbohydrate ingestion during exercise in males and females. *Am J Physiol Endocrinol*  
1153 *Metab.* 2006;290(4):E708-15. doi: 10.1152/ajpendo.00357.2005.
- 1154 83. M'Kaouar H, Péronnet F, Massicotte D, Lavoie C. Gender difference in the metabolic  
1155 response to prolonged exercise with [<sup>13</sup>C]glucose ingestion. *Eur J Appl Physiol.*  
1156 2004;92(4-5):462-9. doi: 10.1007/s00421-004-1122-5.
- 1157 84. Pettersson S, Edin F, Bakkman L, McGawley K. Effects of supplementing with an 18%  
1158 carbohydrate-hydrogel drink versus a placebo during whole-body exercise in -5 °C with  
1159 elite cross-country ski athletes: a crossover study. *J Int Soc Sports Nutr.* 2019;16(1):46.  
1160 doi: 10.1186/s12970-019-0317-4.
- 1161 85. Tremblay J, Peronnet F, Massicotte D, Lavoie C. Carbohydrate supplementation and  
1162 sex differences in fuel selection during exercise. *Med Sci Sports Exerc.*  
1163 2010;42(7):1314-23. doi: 10.1249/MSS.0b013e3181cbba0b.
- 1164 86. Moore DR, Sygo J, Morton JP. Fuelling the female athlete: Carbohydrate and protein  
1165 recommendations. *Eur J Sport Sci.* 2022;22(5):684-96. doi:  
1166 10.1080/17461391.2021.1922508.
- 1167 87. Gagnon DD, Perrier L, Dorman SC, Oddson B, Larivière C, Serresse O. Ambient  
1168 temperature influences metabolic substrate oxidation curves during running and cycling  
1169 in healthy men. *Eur J Sport Sci.* 2020;20(1):90-9. doi:  
1170 10.1080/17461391.2019.1612949.
- 1171 88. Griffiths A, Shannon O, Matu J, King R, Deighton K, O'Hara JP. Response:  
1172 Commentary on the effects of hypoxia on energy substrate use during exercise. *J Int*  
1173 *Soc Sports Nutr.* 2019;16(1):61. doi: 10.1186/s12970-019-0330-7.
- 1174 89. Griffiths A, Shannon OM, Matu J, King R, Deighton K, O'Hara JP. The effects of  
1175 environmental hypoxia on substrate utilisation during exercise: a meta-analysis. *J Int*  
1176 *Soc Sports Nutr.* 2019;16(1):10. doi: 10.1186/s12970-019-0277-8.
- 1177 90. Périard JD, Eijssvogels TMH, Daanen HAM. Exercise under heat stress:  
1178 thermoregulation, hydration, performance implications, and mitigation strategies.  
1179 *Physiol Rev.* 2021;101(4):1873-979. doi: 10.1152/physrev.00038.2020.
- 1180 91. Shearman S, Dwyer D, Skiba P, Townsend N. Modeling Intermittent Cycling  
1181 Performance in Hypoxia Using the Critical Power Concept. *Med Sci Sports Exerc.*  
1182 2016;48(3):527-35. doi: 10.1249/mss.0000000000000794.

- 1183 92. Margolis LM, Wilson MA, Whitney CC, Carrigan CT, Murphy NE, Radcliffe PN, et al.  
1184 Acute hypoxia reduces exogenous glucose oxidation, glucose turnover, and metabolic  
1185 clearance rate during steady-state aerobic exercise. *Metabolism*. 2020;103:154030. doi:  
1186 10.1016/j.metabol.2019.154030.
- 1187 93. Young AJ, Berryman CE, Kenefick RW, Derosier AN, Margolis LM, Wilson MA, et al.  
1188 Altitude Acclimatization Alleviates the Hypoxia-Induced Suppression of Exogenous  
1189 Glucose Oxidation During Steady-State Aerobic Exercise. *Front Physiol*. 2018;9:830.  
1190 doi: 10.3389/fphys.2018.00830.
- 1191 94. O'Hara JP, Woods DR, Mellor A, Boos C, Gallagher L, Tsakirides C, et al. A comparison  
1192 of substrate oxidation during prolonged exercise in men at terrestrial altitude and  
1193 normobaric normoxia following the coingestion of <sup>13</sup>C glucose and <sup>13</sup>C fructose.  
1194 *Physiol Rep*. 2017;5(1). doi: 10.14814/phy2.13101.
- 1195 95. Mujika I, Sharma AP, Stellingwerff T. Contemporary Periodization of Altitude Training  
1196 for Elite Endurance Athletes: A Narrative Review. *Sports Med*. 2019;49(11):1651-69.  
1197 doi: 10.1007/s40279-019-01165-y.
- 1198 96. Febbraio MA, Snow RJ, Hargreaves M, Stathis CG, Martin IK, Carey MF. Muscle  
1199 metabolism during exercise and heat stress in trained men: effect of acclimation. *J Appl*  
1200 *Physiol* (1985). 1994;76(2):589-97. doi: 10.1152/jappl.1994.76.2.589.
- 1201 97. Febbraio MA, Snow RJ, Stathis CG, Hargreaves M, Carey MF. Effect of heat stress on  
1202 muscle energy metabolism during exercise. *J Appl Physiol* (1985). 1994;77(6):2827-  
1203 31. doi: 10.1152/jappl.1994.77.6.2827.
- 1204 98. Jentjens RL, Wagenmakers AJ, Jeukendrup AE. Heat stress increases muscle glycogen  
1205 use but reduces the oxidation of ingested carbohydrates during exercise. *J Appl Physiol*  
1206 (1985). 2002;92(4):1562-72. doi: 10.1152/jappphysiol.00482.2001.
- 1207 99. King DS, Costill DL, Fink WJ, Hargreaves M, Fielding RA. Muscle metabolism during  
1208 exercise in the heat in unacclimatized and acclimatized humans. *J Appl Physiol* (1985).  
1209 1985;59(5):1350-4. doi: 10.1152/jappl.1985.59.5.1350.
- 1210 100. Reynolds KM, Funnell MP, Collins AJ, Mears SA, Pugh JN, James LJ. A Warm  
1211 Environment Reduces Exogenous Glucose Oxidation and Endurance Performance  
1212 during Cycling with Facing Airflow. *Med Sci Sports Exerc*. 2025;57(5):1043-55. doi:  
1213 10.1249/mss.0000000000003632.
- 1214 101. Mougins L, Horner M, Edwards D, Nickels M, Taylor L, James LJ, et al. Heat stress  
1215 impairs exogenous carbohydrate oxidation during prolonged running when maintaining  
1216 euhydration. *Journal of Applied Physiology*. 2025;0(0):null. doi:  
1217 10.1152/jappphysiol.00873.2025.
- 1218 102. Rosbrook P, Looney DP, Margolis LM, Yudin SP, Hostler D, Pryor RR, et al. Dietary  
1219 Carbohydrates Influence the Performance Outcomes of Short-Term Heat Acclimation.  
1220 *Med Sci Sports Exerc*. 2025;57(9):1947-57. doi: 10.1249/mss.0000000000003726.
- 1221 103. Hurley BF, Haymes EM. The effects of rest and exercise in the cold on substrate  
1222 mobilization and utilization. *Aviat Space Environ Med*. 1982;53(12):1193-7.

- 1223 104. Ito R, Nakano M, Yamane M, Amano M, Matsumoto T. Effects of rain on energy  
1224 metabolism while running in a cold environment. *Int J Sports Med.* 2013;34(8):707-11.  
1225 doi: 10.1055/s-0032-1331770.
- 1226 105. Ito R, Yamashita N. Moderately cool environment with rain and wind increases cold  
1227 strain and energy expenditure via carbohydrate oxidation during running exercise. *J*  
1228 *Sports Med Phys Fitness.* 2025;65(2):180-7. doi: 10.23736/s0022-4707.24.16100-2.
- 1229 106. Galloway SD, Wootton SA, Murphy JL, Maughan RJ. Exogenous carbohydrate  
1230 oxidation from drinks ingested during prolonged exercise in a cold environment in  
1231 humans. *J Appl Physiol (1985).* 2001;91(2):654-60. doi: 10.1152/jappl.2001.91.2.654.
- 1232 107. Passias TC, Meneilly GS, Mekjavić IB. Effect of hypoglycemia on thermoregulatory  
1233 responses. *J Appl Physiol (1985).* 1996;80(3):1021-32. doi:  
1234 10.1152/jappl.1996.80.3.1021.
- 1235 108. Costa RJS, Snipe RMJ, Kitic CM, Gibson PR. Systematic review: exercise-induced  
1236 gastrointestinal syndrome-implications for health and intestinal disease. *Alimentary*  
1237 *pharmacology & therapeutics.* 2017;46(3):246-65. doi: 10.1111/apt.14157.
- 1238 109. Pugh JN, Kirk B, Fearn R, Morton JP, Close GL. Prevalence, Severity and Potential  
1239 Nutritional Causes of Gastrointestinal Symptoms during a Marathon in Recreational  
1240 Runners. *Nutrients.* 2018;10(7). doi: 10.3390/nu10070811.
- 1241 110. Peters HP, Bos M, Seebregts L, Akkermans LM, van Berge Henegouwen GP, Bol E, et  
1242 al. Gastrointestinal symptoms in long-distance runners, cyclists, and triathletes:  
1243 prevalence, medication, and etiology. *Am J Gastroenterol.* 1999;94(6):1570-81. doi:  
1244 10.1111/j.1572-0241.1999.01147.x.
- 1245 111. Stuempfle KJ, Hoffman MD. Gastrointestinal distress is common during a 161-km  
1246 ultramarathon. *Journal of sports sciences.* 2015;33(17):1814-21. doi:  
1247 10.1080/02640414.2015.1012104.
- 1248 112. ter Steege RW, Kolkman JJ. Review article: the pathophysiology and management of  
1249 gastrointestinal symptoms during physical exercise, and the role of splanchnic blood  
1250 flow. *Alimentary pharmacology & therapeutics.* 2012;35(5):516-28. doi:  
1251 10.1111/j.1365-2036.2011.04980.x.
- 1252 113. de Oliveira EP, Burini RC, Jeukendrup A. Gastrointestinal complaints during exercise:  
1253 prevalence, etiology, and nutritional recommendations. *Sports medicine (Auckland,*  
1254 *NZ).* 2014;44 Suppl 1(Suppl 1):S79-85. doi: 10.1007/s40279-014-0153-2.
- 1255 114. Snipe RMJ, Khoo A, Kitic CM, Gibson PR, Costa RJS. The impact of exertional-heat  
1256 stress on gastrointestinal integrity, gastrointestinal symptoms, systemic endotoxin and  
1257 cytokine profile. *Eur J Appl Physiol.* 2018;118(2):389-400. doi: 10.1007/s00421-017-  
1258 3781-z.
- 1259 115. Walter E, Gibson OR, Stacey M, Hill N, Parsons IT, Woods D. Changes in  
1260 gastrointestinal cell integrity after marathon running and exercise-associated collapse.  
1261 *Eur J Appl Physiol.* 2021;121(4):1179-87. doi: 10.1007/s00421-021-04603-w.

- 1262 116. Brock-Utne JG, Gaffin SL, Wells MT, Gathiram P, Sohar E, James MF, et al.  
1263 Endotoxaemia in exhausted runners after a long-distance race. *S Afr Med J*.  
1264 1988;73(9):533-6.
- 1265 117. Lambert GP, Broussard LJ, Mason BL, Mauermann WJ, Gisolfi CV. Gastrointestinal  
1266 permeability during exercise: effects of aspirin and energy-containing beverages.  
1267 *Journal of applied physiology* (Bethesda, Md : 1985). 2001;90(6):2075-80. doi:  
1268 10.1152/jappl.2001.90.6.2075.
- 1269 118. Snipe RMJ, Khoo A, Kitic CM, Gibson PR, Costa RJS. Carbohydrate and protein intake  
1270 during exertional heat stress ameliorates intestinal epithelial injury and small intestine  
1271 permeability. *Appl Physiol Nutr Metab*. 2017;42(12):1283-92. doi: 10.1139/apnm-  
1272 2017-0361.
- 1273 119. Jonvik KL, Lenaerts K, Smeets JSJ, Kolkman JJ, LJC VANL, Verdijk LB. Sucrose but  
1274 Not Nitrate Ingestion Reduces Strenuous Cycling-induced Intestinal Injury. *Medicine*  
1275 and science in sports and exercise. 2019;51(3):436-44. doi:  
1276 10.1249/mss.0000000000001800.
- 1277 120. Rehrer NJ, Wagenmakers AJ, Beckers EJ, Halliday D, Leiper JB, Brouns F, et al.  
1278 Gastric emptying, absorption, and carbohydrate oxidation during prolonged exercise.  
1279 *Journal of applied physiology* (Bethesda, Md : 1985). 1992;72(2):468-75. doi:  
1280 10.1152/jappl.1992.72.2.468.
- 1281 121. Martinez IG, Mika AS, Biesiekierski JR, Costa RJS. The Effect of Gut-Training and  
1282 Feeding-Challenge on Markers of Gastrointestinal Status in Response to Endurance  
1283 Exercise: A Systematic Literature Review. *Sports medicine* (Auckland, NZ).  
1284 2023;53(6):1175-200. doi: 10.1007/s40279-023-01841-0.
- 1285 122. Lambert GP, Lang J, Bull A, Eckerson J, Lanspa S, O'Brien J. Fluid tolerance while  
1286 running: effect of repeated trials. *International journal of sports medicine*.  
1287 2008;29(11):878-82. doi: 10.1055/s-2008-1038620.
- 1288 123. King AJ, Etxebarria N, Ross ML, Garvican-Lewis L, Heikura IA, McKay AKA, et al.  
1289 Short-Term Very High Carbohydrate Diet and Gut-Training Have Minor Effects on  
1290 Gastrointestinal Status and Performance in Highly Trained Endurance Athletes.  
1291 *Nutrients*. 2022;14(9). doi: 10.3390/nu14091929.
- 1292 124. Costa RJS, Miall A, Khoo A, Rauch C, Snipe R, Camões-Costa V, et al. Gut-training:  
1293 the impact of two weeks repetitive gut-challenge during exercise on gastrointestinal  
1294 status, glucose availability, fuel kinetics, and running performance. *Appl Physiol Nutr*  
1295 *Metab*. 2017;42(5):547-57. doi: 10.1139/apnm-2016-0453.
- 1296 125. Miall A, Khoo A, Rauch C, Snipe RMJ, Camões-Costa VL, Gibson PR, et al. Two  
1297 weeks of repetitive gut-challenge reduce exercise-associated gastrointestinal symptoms  
1298 and malabsorption. *Scand J Med Sci Sports*. 2018;28(2):630-40. doi:  
1299 10.1111/sms.12912.
- 1300 126. Cox AJ, Pyne DB, Cox GR, Callister R, Gleeson M. Influence of chronic dietary  
1301 carbohydrate supplementation on plasma cytokine responses to exercise. *International*  
1302 *journal of sports medicine*. 2010;31(3):207-12. doi: 10.1055/s-0029-1243645.

- 1303 127. Ijaz A, Collins AJ, Moreno-Cabañas A, Bradshaw L, Hutchins K, Betts JA, et al.  
1304 Exogenous Glucose Oxidation During Exercise Is Positively Related to Body Size. *Int*  
1305 *J Sport Nutr Exerc Metab.* 2025;35(1):12-23. doi: 10.1123/ijsnem.2024-0097.
- 1306 128. Podlogar T, Cooper-Smith N, Gonzalez JT, Wallis GA. Personalised carbohydrate  
1307 feeding during exercise based on exogenous glucose oxidation: a proof-of-concept  
1308 study. *Performance Nutrition.* 2025;1(1):2. doi: 10.1186/s44410-025-00003-9.
- 1309 129. Massicotte D, Péronnet F, Adopo E, Brisson GR, Hillaire-Marcel C. Effect of metabolic  
1310 rate on the oxidation of ingested glucose and fructose during exercise. *Int J Sports Med.*  
1311 1994;15(4):177-80. doi: 10.1055/s-2007-1021043.
- 1312 130. Wallis GA, Rowlands DS, Shaw C, Jentjens RL, Jeukendrup AE. Oxidation of  
1313 combined ingestion of maltodextrins and fructose during exercise. *Med Sci Sports*  
1314 *Exerc.* 2005;37(3):426-32. doi: 10.1249/01.mss.0000155399.23358.82.
- 1315 131. Hunter B, Maunder E, Jones AM, Gallo G, Muniz-Pumares D. Durability as an index  
1316 of endurance exercise performance: Methodological considerations. *Exp Physiol.*  
1317 2025;110(11):1612-24. doi: 10.1113/ep092120.
- 1318 132. Clark IE, Vanhatalo A, Thompson C, Joseph C, Black MI, Blackwell JR, et al.  
1319 Dynamics of the power-duration relationship during prolonged endurance exercise and  
1320 influence of carbohydrate ingestion. *J Appl Physiol (1985).* 2019;127(3):726-36. doi:  
1321 10.1152/jappphysiol.00207.2019.
- 1322 133. Ørtenblad N, Zachariassen M, Nielsen J, Gejl KD. Substrate utilization and durability  
1323 during prolonged intermittent exercise in elite road cyclists. *Eur J Appl Physiol.*  
1324 2024;124(7):2193-205. doi: 10.1007/s00421-024-05437-y.
- 1325 134. Spragg J, Leo P, Swart J. The Relationship between Physiological Characteristics and  
1326 Durability in Male Professional Cyclists. *Med Sci Sports Exerc.* 2023;55(1):133-40.  
1327 doi: 10.1249/mss.0000000000003024.
- 1328 135. Morton JP, Hearn M, Fell MJ, Owens DJ, Halson S, Trommelen J. UCI Sports  
1329 Nutrition Project: Nutritional Periodization: Strategies to Enhance Training Adaptation  
1330 and Recovery. *Int J Sport Nutr Exerc Metab.* 2025:1-26. doi: 10.1123/ijsnem.2025-  
1331 0073.
- 1332 136. García-Rovés PM, Terrados N, Fernández SF, Patterson AM. Macronutrients intake of  
1333 top level cyclists during continuous competition--change in the feeding pattern. *Int J*  
1334 *Sports Med.* 1998;19(1):61-7. doi: 10.1055/s-2007-971882.
- 1335 137. Muros JJ, Sánchez-Muñoz C, Hoyos J, Zabala M. Nutritional intake and body  
1336 composition changes in a UCI World Tour cycling team during the Tour of Spain. *Eur*  
1337 *J Sport Sci.* 2019;19(1):86-94. doi: 10.1080/17461391.2018.1497088.
- 1338 138. Saris WH, van Erp-Baart MA, Brouns F, Westerterp KR, ten Hoor F. Study on food  
1339 intake and energy expenditure during extreme sustained exercise: the Tour de France.  
1340 *Int J Sports Med.* 1989;10 Suppl 1:S26-31. doi: 10.1055/s-2007-1024951.
- 1341 139. Ross ML, Stephens B, Abbiss CR, Martin DT, Laursen PB, Burke LM. Fluid balance,  
1342 carbohydrate ingestion, and body temperature during men's stage-race cycling in

- 1343 temperate environmental conditions. *Int J Sports Physiol Perform.* 2014;9(3):575-82.  
1344 doi: 10.1123/ijsp.2012-0369.
- 1345 140. Plasqui G, Rietjens G, Lambriks L, Wouters L, Saris WHM. Energy Expenditure during  
1346 Extreme Endurance Exercise: The Giro d'Italia. *Med Sci Sports Exerc.* 2019;51(3):568-  
1347 74. doi: 10.1249/mss.0000000000001814.
- 1348 141. van Erp T, Foster C, de Koning JJ. Relationship Between Various Training-Load  
1349 Measures in Elite Cyclists During Training, Road Races, and Time Trials. *Int J Sports  
1350 Physiol Perform.* 2019;14(4):493-500. doi: 10.1123/ijsp.2017-0722.
- 1351 142. Van Erp T, Sanders D. Demands of professional cycling races: Influence of race  
1352 category and result. *Eur J Sport Sci.* 2021;21(5):666-77. doi:  
1353 10.1080/17461391.2020.1788651.
- 1354 143. Van Hooren B, Cox M, Rietjens G, Plasqui G. Determination of energy expenditure in  
1355 professional cyclists using power data: Validation against doubly labeled water. *Scand  
1356 J Med Sci Sports.* 2023;33(4):407-19. doi: 10.1111/sms.14271.
- 1357 144. Peeters WM, Barrett M, Podlogar T. What is a cycling race simulation anyway: a review  
1358 on protocols to assess durability in cycling. *Eur J Appl Physiol.* 2025;125(6):1527-48.  
1359 doi: 10.1007/s00421-025-05725-1.
- 1360 145. Jiménez-Alfageme R, Garrone FP, Rodríguez-Sánchez N, Romero-García D, Sospedra  
1361 I, Giménez-Monzó D, et al. Nutritional Intake and Timing of Marathon Runners:  
1362 Influence of Athlete's Characteristics and Fueling Practices on Finishing Time. *Sports  
1363 Med Open.* 2025;11(1):26. doi: 10.1186/s40798-024-00801-w.
- 1364 146. Sampson G, Morton JP, Areta JL. A broken link: Knowledge of carbohydrate  
1365 requirements do not predict carbohydrate intake around competition in endurance  
1366 athletes. *Eur J Sport Sci.* 2024;24(10):1395-404. doi: 10.1002/ejsc.12183.
- 1367 147. Costa RJS, Young P, Gill SK, Snipe RMJ, Gaskell S, Russo I, et al. Assessment of  
1368 Exercise-Associated Gastrointestinal Perturbations in Research and Practical Settings:  
1369 Methodological Concerns and Recommendations for Best Practice. *Int J Sport Nutr  
1370 Exerc Metab.* 2022;32(5):387-418. doi: 10.1123/ijsnem.2022-0048.
- 1371 148. Lukasiewicz CJ, Vandiver KJ, Albert ED, Kirby BS, Jacobs RA. Assessing exogenous  
1372 carbohydrate intake needed to optimize human endurance performance across sex:  
1373 insights from modeling runners pursuing a sub-2-h marathon. *J Appl Physiol (1985).*  
1374 2024;136(1):158-76. doi: 10.1152/jappphysiol.00521.2023.
- 1375 149. Leckey JJ, Burke LM, Morton JP, Hawley JA. Altering fatty acid availability does not  
1376 impair prolonged, continuous running to fatigue: evidence for carbohydrate  
1377 dependence. *J Appl Physiol (1985).* 2016;120(2):107-13. doi:  
1378 10.1152/jappphysiol.00855.2015.
- 1379 150. O'Brien MJ, Viguie CA, Mazzeo RS, Brooks GA. Carbohydrate dependence during  
1380 marathon running. *Med Sci Sports Exerc.* 1993;25(9):1009-17.

- 1381 151. Costa RJS, Knechtle B, Tarnopolsky M, Hoffman MD. Nutrition for Ultramarathon  
1382 Running: Trail, Track, and Road. *Int J Sport Nutr Exerc Metab.* 2019;29(2):130-40. doi:  
1383 10.1123/ijsnem.2018-0255.
- 1384 152. Scheer V. Participation Trends of Ultra Endurance Events. *Sports Med Arthrosc Rev.*  
1385 2019;27(1):3-7. doi: 10.1097/jsa.000000000000198.
- 1386 153. Rowlands DS, Houltham SD. Multiple-Transportable Carbohydrate Effect on Long-  
1387 Distance Triathlon Performance. *Med Sci Sports Exerc.* 2017;49(8):1734-44. doi:  
1388 10.1249/mss.0000000000001278.
- 1389 154. Peters HP, van Schelven FW, Verstappen PA, de Boer RW, Bol E, Erich WB, et al.  
1390 Gastrointestinal problems as a function of carbohydrate supplements and mode of  
1391 exercise. *Med Sci Sports Exerc.* 1993;25(11):1211-24.
- 1392 155. Pfeiffer B, Stellingwerff T, Zaltas E, Hodgson AB, Jeukendrup AE. Carbohydrate  
1393 oxidation from a drink during running compared with cycling exercise. *Med Sci Sports  
1394 Exerc.* 2011;43(2):327-34. doi: 10.1249/MSS.0b013e3181ebc488.
- 1395 156. Rehrer NJ, Beckers EJ, Brouns F, ten Hoor F, Saris WH. Effects of dehydration on  
1396 gastric emptying and gastrointestinal distress while running. *Med Sci Sports Exerc.*  
1397 1990;22(6):790-5. doi: 10.1249/00005768-199012000-00010.
- 1398 157. Mougín L, Macrae HZ, Taylor L, James LJ, Mears SA. The Effect of Heat Stress and  
1399 Dehydration on Carbohydrate Use During Endurance Exercise: A Systematic Review  
1400 and Meta-Analysis. *Sports Med.* 2025;55(11):2825-47. doi: 10.1007/s40279-025-  
1401 02294-3.
- 1402 158. Fornasiero A, Savoldelli A, Fruet D, Boccia G, Pellegrini B, Schena F. Physiological  
1403 intensity profile, exercise load and performance predictors of a 65-km mountain ultra-  
1404 marathon. *Journal of sports sciences.* 2018;36(11):1287-95. doi:  
1405 10.1080/02640414.2017.1374707.
- 1406 159. Millet GY, Banfi JC, Kerherve H, Morin JB, Vincent L, Estrade C, et al. Physiological  
1407 and biological factors associated with a 24 h treadmill ultra-marathon performance.  
1408 *Scandinavian journal of medicine & science in sports.* 2011;21(1):54-61. doi:  
1409 10.1111/j.1600-0838.2009.01001.x.
- 1410 160. Barrero A, Chaverri D, Erola P, Iglesias X, Rodríguez FA. Intensity profile during an  
1411 ultra-endurance triathlon in relation to testing and performance. *International journal of  
1412 sports medicine.* 2014;35(14):1170-8. doi: 10.1055/s-0034-1374601.
- 1413 161. Dumke CL, Shooter L, Lind RH, Nieman DC. Indirect calorimetry during ultradistance  
1414 running: a case report. *J Sports Sci Med.* 2006;5(4):692-8.
- 1415 162. Stellingwerff T. Competition Nutrition Practices of Elite Ultramarathon Runners. *Int J  
1416 Sport Nutr Exerc Metab.* 2016;26(1):93-9. doi: 10.1123/ijsnem.2015-0030.
- 1417 163. Christensen PM. Aerobic Energy Turnover and Exercise Economy Profile During Race  
1418 Simulation in a World-Record-Breaking Male Full-Distance Triathlete. *Int J Sports  
1419 Physiol Perform.* 2025;20(1):161-7. doi: 10.1123/ijspp.2024-0221.

- 1420 164. Noakes T, Buga A, Volek J, Prins P. Identification of a reverse crossover point during  
1421 moderate-intensity exercise (>6 h; 69% VO<sub>2</sub>max) in a world-class triathlete-A  
1422 secondary analysis. *Front Nutr.* 2025;12:1627404. doi: 10.3389/fnut.2025.1627404.
- 1423 165. Frandsen J, Vest SD, Larsen S, Dela F, Helge JW. Maximal Fat Oxidation is Related to  
1424 Performance in an Ironman Triathlon. *International journal of sports medicine.*  
1425 2017;38(13):975-82. doi: 10.1055/s-0043-117178.
- 1426 166. Stuempfle KJ, Hoffman MD, Weschler LB, Rogers IR, Hew-Butler T. Race diet of  
1427 finishers and non-finishers in a 100 mile (161 km) mountain footrace. *J Am Coll Nutr.*  
1428 2011;30(6):529-35. doi: 10.1080/07315724.2011.10719999.
- 1429 167. Glace BW, Murphy CA, McHugh MP. Food intake and electrolyte status of  
1430 ultramarathoners competing in extreme heat. *J Am Coll Nutr.* 2002;21(6):553-9. doi:  
1431 10.1080/07315724.2002.10719254.
- 1432 168. Inamura N, Taniguchi H, Yoshida S, Nishioka M, Ishihara K. A comparative  
1433 observational study of carbohydrate intake and continuous blood glucose levels in  
1434 relation to performance in ultramarathon. *Scientific Reports.* 2024;14(1):1089. doi:  
1435 10.1038/s41598-023-51048-6.
- 1436 169. Kinrade EJ, Galloway SDR. Dietary Observations of Ultra-Endurance Runners in  
1437 Preparation for and During a Continuous 24-h Event. *Front Physiol.* 2021;12:765888.  
1438 doi: 10.3389/fphys.2021.765888.
- 1439 170. Costa RJ, Gill SK, Hankey J, Wright A, Marczak S. Perturbed energy balance and  
1440 hydration status in ultra-endurance runners during a 24 h ultra-marathon. *Br J Nutr.*  
1441 2014;112(3):428-37. doi: 10.1017/s0007114514000907.
- 1442 171. Martinez S, Aguilo A, Rodas L, Lozano L, Moreno C, Tauler P. Energy, macronutrient  
1443 and water intake during a mountain ultramarathon event: The influence of distance. *J*  
1444 *Sports Sci.* 2018;36(3):333-9. doi: 10.1080/02640414.2017.1306092.
- 1445 172. Wardenaar FC, Hoogervorst D, Versteegen JJ, van der Burg N, Lambrechtse KJ,  
1446 Bongers C. Real-Time Observations of Food and Fluid Timing During a 120 km  
1447 Ultramarathon. *Front Nutr.* 2018;5:32. doi: 10.3389/fnut.2018.00032.
- 1448 173. Blennerhassett C, McNaughton LR, Sparks SA. Factors influencing ultra-endurance  
1449 athletes food choices: an adapted food choice questionnaire. *Res Sports Med.*  
1450 2019;27(2):257-71. doi: 10.1080/15438627.2018.1530999.
- 1451 174. Glace B, Murphy C, McHugh M. Food and fluid intake and disturbances in  
1452 gastrointestinal and mental function during an ultramarathon. *Int J Sport Nutr Exerc*  
1453 *Metab.* 2002;12(4):414-27. doi: 10.1123/ijsnem.12.4.414.
- 1454 175. Costa RJ, Snipe R, Camões-Costa V, Scheer V, Murray A. The Impact of  
1455 Gastrointestinal Symptoms and Dermatological Injuries on Nutritional Intake and  
1456 Hydration Status During Ultramarathon Events. *Sports Med Open.* 2016;2:16. doi:  
1457 10.1186/s40798-015-0041-9.

- 1458 176. Lavoué C, Siracusa J, Chalchat É, Bourrilhon C, Charlot K. Analysis of food and fluid  
1459 intake in elite ultra-endurance runners during a 24-h world championship. *J Int Soc*  
1460 *Sports Nutr.* 2020;17(1):36. doi: 10.1186/s12970-020-00364-7.
- 1461 177. Rontoyannis GP, Skoulis T, Pavlou KN. Energy balance in ultramarathon running. *Am*  
1462 *J Clin Nutr.* 1989;49(5 Suppl):976-9. doi: 10.1093/ajcn/49.5.976.
- 1463 178. Viribay A, Arribalzaga S, Mielgo-Ayuso J, Castañeda-Babarro A, Seco-Calvo J,  
1464 Urdampilleta A. Effects of 120 g/h of Carbohydrates Intake during a Mountain  
1465 Marathon on Exercise-Induced Muscle Damage in Elite Runners. *Nutrients.*  
1466 2020;12(5). doi: 10.3390/nu12051367.
- 1467 179. Krabel H. *What The Pros Are Eating: Men of WSER* [Internet]. Freerail; 2024;  
1468 Available from: <https://freerail.com/what-the-pros-are-eating-men-of-wser/>.
- 1469 180. Close GL, Kasper AM, Morton JP. From Paper to Podium: Quantifying the  
1470 Translational Potential of Performance Nutrition Research. *Sports Med.* 2019;49(Suppl  
1471 1):25-37. doi: 10.1007/s40279-018-1005-2.
- 1472 181. Burke LM, Whitfield J, Hawley JA. The race within a race: Together on the marathon  
1473 starting line but miles apart in the experience. *Free Radic Biol Med.* 2025;227:367-78.  
1474 doi: 10.1016/j.freeradbiomed.2024.10.277.
- 1475 182. McKay AKA, Stellingwerff T, Smith ES, Martin DT, Mujika I, Goosey-Tolfrey VL, et  
1476 al. Defining Training and Performance Caliber: A Participant Classification  
1477 Framework. *Int J Sports Physiol Perform.* 2022;17(2):317-31. doi: 10.1123/ijsp.2021-  
1478 0451.
- 1479 183. Yaspelkis BB, 3rd, Patterson JG, Anderla PA, Ding Z, Ivy JL. Carbohydrate  
1480 supplementation spares muscle glycogen during variable-intensity exercise. *J Appl*  
1481 *Physiol* (1985). 1993;75(4):1477-85. doi: 10.1152/jappl.1993.75.4.1477.
- 1482 184. Jones RO, Vaz DEOM, Palmer B, Maguire D, Butler G, Gothard I, et al. Different  
1483 Carbohydrate Ingestion Patterns Do Not Affect Physiological Responses, Whole-Body  
1484 Substrate Oxidation or Gastrointestinal Comfort in Cycling. *Eur J Sport Sci.*  
1485 2025;25(7):e12336. doi: 10.1002/ejsc.12336.  
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1517 **Table 1.** Emerging practitioner relevant nutrition considerations and future research needs for  
 1518 prescribing and assessing CHO intake of cyclists in stage and race settings.

Practical Nutrition Consideration or Area of Future Research	Context	Scientific Reference
Is it plausible that muscle glycogen synthesis occurs during races or stages?	Owing to the variable intensity of road cycling, riders may spend extended periods at low power in the peloton or freewheeling on long descents. During these phases, CHO intake may support some degree of glycogen resynthesis, as reduced muscular demand allows a portion of ingested CHO to be directed towards glycogen synthesis rather than immediate oxidation.	Kuipers, et al. (50) Yaspelkis, et al. (183)

Implications for estimating CHO intake during races or stages	In-race CHO intake is often estimated from riders' self-reported consumption of pre-packaged sports foods and drinks. This approach may overestimate actual CHO intake by ignoring residual product in wrappers, partially consumed gels and unfinished bottles.	Lanpir, et al. (79)
Does CHO feeding pattern influence metabolic and physiological responses during races or stages?	Practitioners often calculate average hourly CHO intake by dividing total CHO consumed by stage duration. This assumes a constant intake rate, which rarely reflects the reality of racing. Attacks, weather, and tactical moments can create substantial hour-to-hour variation in CHO intake. The physiological consequences of these fluctuations, and of different ingestion strategies (e.g. large infrequent boluses, regular moderate feedings, or continuous small "drip" feeding), remain unclear.	Jones, et al. (184)

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1529 **Figure 1** – The effects of CHO ingestion during exercise on the contribution of CHO and fat  
 1530 to substrate metabolism. Data are redrawn and compiled from studies where male cyclists  
 1531 performed 3 h of sub-maximal exercise at 95% of lactate threshold and ingested 0 (**A**), 45 (**B**),  
 1532 90 (**C**) or 120 g·h<sup>-1</sup> (**D**). Note that ingestion rates of 45 and 90 g·h<sup>-1</sup> only *delays* the time to  
 1533 “crossover” compared with no CHO ingestion as indicated by the arrow on each panel. In  
 1534 contrast, 120 g·h<sup>-1</sup> *prevents* the crossover point and CHO remains the predominant substrate.  
 1535 Panels A-C, Fell, et al. (34); Panel D, Hearnis, et al. (23).

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1537 **Figure 2** – The effects of fructose-glucose ratio on rates of exogenous CHO oxidation during  
 1538 exercise. Data are redrawn and compiled from studies where male cyclists performed 2.5 h of  
 1539 sub-maximal exercise at 50% PPO (21, 72) or 2 h at 57% PPO (73).

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1541 **Figure 3** – CHO intake of the 2018 Giro d'Italia winner Chris Froome during Stage 11 to 19  
 1542 expressed in **(A)**  $\text{g}\cdot\text{h}^{-1}$  and **(B)** absolute quantity of CHO consumed from semi-solids (i.e. gels),  
 1543 solids (i.e. bars and rice cakes) and fluids (Morton, personal communication). **(C)** CHO intake  
 1544 of a World Tour cyclist during Stage 3-20 of the 2023 Tour de France (Fell, personal  
 1545 communication). Stage types are categorised as, F: Flat stage; H: Hilly stage; MT: Mountain  
 1546 Stage; ITT: Individual Time Trial Stage.

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1548 **Figure 4** – The effects of CHO ingestion (at rates of 60, 90 and  $120 \text{ g}\cdot\text{h}^{-1}$ ) during running on  
 1549 **(A)** whole-body rates of CHO oxidation, **(B)** exogenous CHO oxidation and **(C)**, running  
 1550 economy. Data are redrawn from Ravikanti, et al. (35) and are representative of trained male  
 1551 runners completing 2 h of treadmill running (an initial 15-min period at 95% of LT, a  
 1552 subsequent 90-min period at 94% of LTP and a final 15-min period at 95% of LT). In the second  
 1553 hour of exercise, the contribution of CHO towards total energy expenditure was significantly different  
 1554 between conditions such that CHO accounted for 65, 51 and 43% in the 120, 90 and  $60 \text{ g}\cdot\text{h}^{-1}$  trials,  
 1555 respectively.

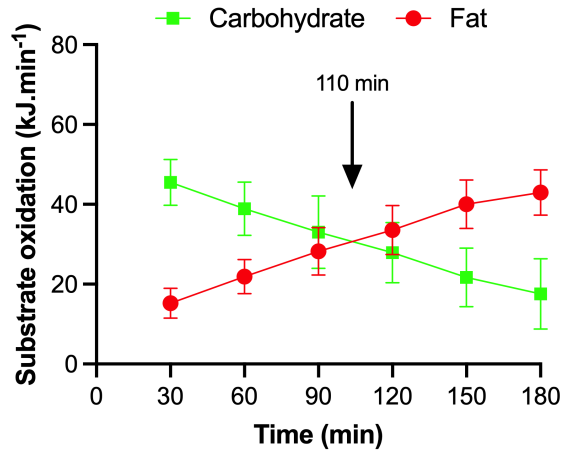
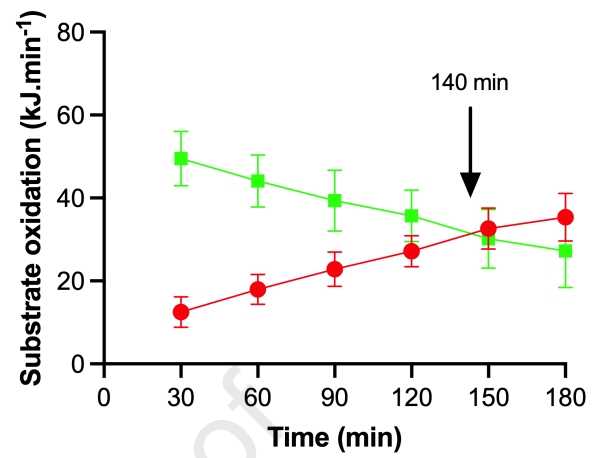
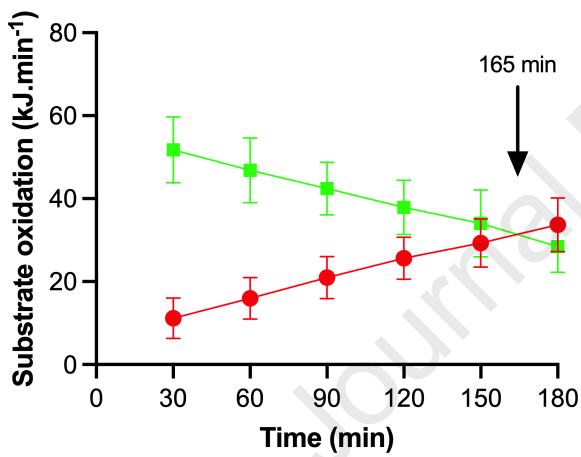
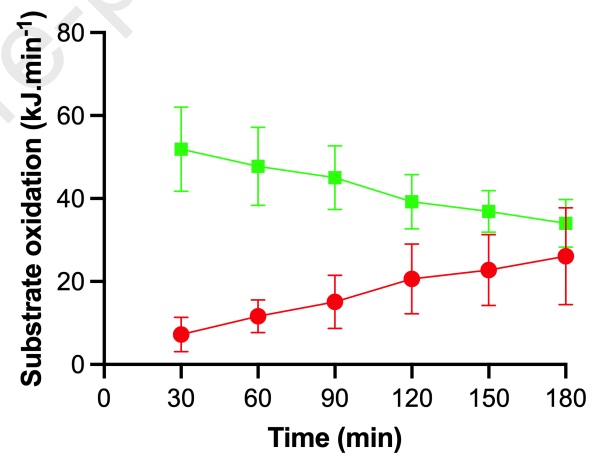
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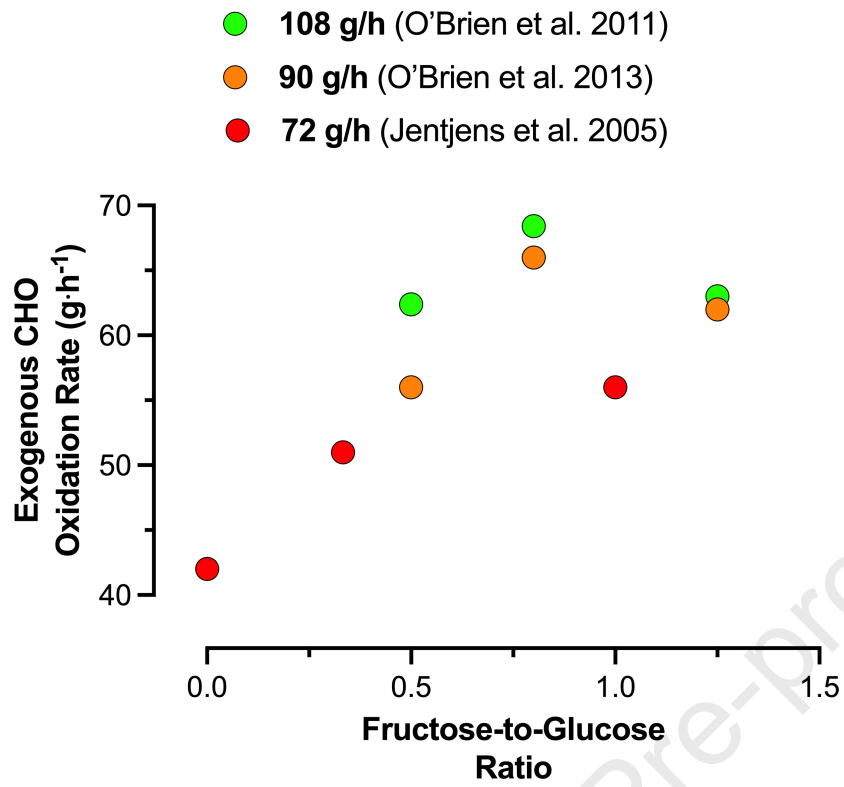
1557 **Figure 5** – Theoretical model to guide CHO feeding strategies for endurance athletes. This  
 1558 model considers the absolute quantity (i.e.  $\text{g}\cdot\text{h}^{-1}$ ) and format of CHO ingestion (i.e. drinks, gels,  
 1559 chews, bars) that may be best suited to maintaining the whole-body rates of CHO oxidation  
 1560 that may sustain the target exercise intensity (and economy / efficiency / durability etc) for the  
 1561 required exercise duration and thereby optimise performance. Exercise intensity is depicted  
 1562 according to 3 common approaches such as exercise intensity domains, % of  $\text{VO}_{2\text{max}}$  and  
 1563 endurance training zones, where upward and downward arrows are indicative of the range of  
 1564 intensities and rates of CHO oxidation associated with each sporting scenario. Similarly,  
 1565 exercise duration is segmented to hourly zones where rightward arrows are indicative of the  
 1566 range of durations associated with each sporting scenario. It is noted that the absolute rates of  
 1567 whole-body CHO oxidation and the range of associated exercise intensities and exercise  
 1568 durations are representative of published data from male athletes that span the training status  
 1569 of Tier 2 (Trained / Developmental), 3 (Highly Trained / National), 4 (Elite / International  
 1570 Level) and 5 (World Class) athletes (McKay et al. 2022). Accordingly, absolute rates of CHO  
 1571 oxidation are likely not applicable for female athletes and further research is required to address  
 1572 this gap (see Section 6).

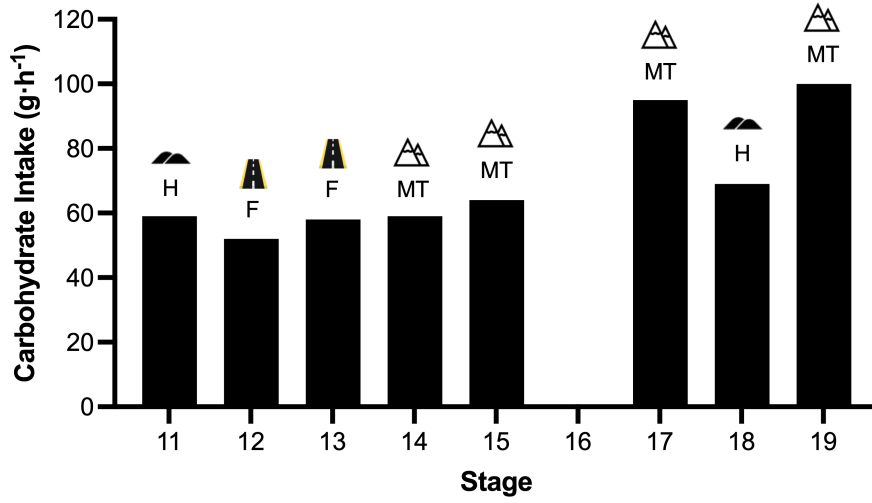
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1574 **Figure 6** – Absolute rate of CHO and fat utilisation and contribution of CHO and fat to whole-  
 1575 body substrate metabolism in a Tier 5 Ethiopian male **(A and B)**, respectively) and female  
 1576 marathon runner **(C and D)**, respectively). Data were collected during incremental exercise  
 1577 testing (3-min stages) on a motorised treadmill set at 1% incline (Pulsar H/p, Cosmos,  
 1578 Germany) in the corresponding author's laboratory, where substrate utilisation was assessed  
 1579 according to indirect calorimetry (Moxus Modular Metabolic System, AEI Technologies,  
 1580 USA). Such data demonstrate the high capacity for fat oxidation in world class athletes, even  
 1581 when running at the absolute speeds associated with marathon race pace.

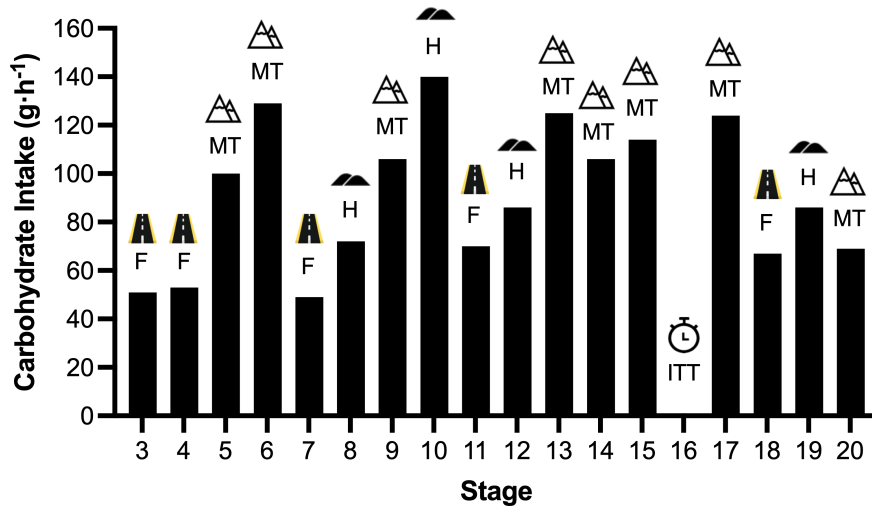
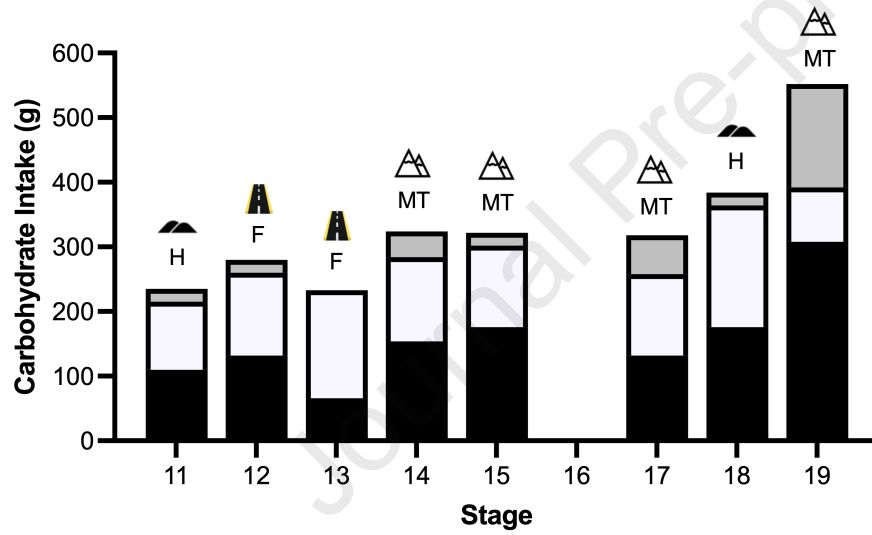
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**A: 0 g.h<sup>-1</sup>****B: 45 g.h<sup>-1</sup>****C: 90 g.h<sup>-1</sup>****D: 120 g.h<sup>-1</sup>**

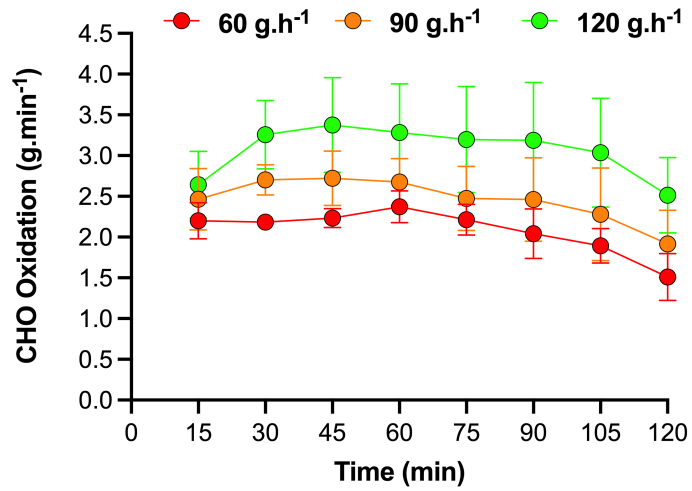




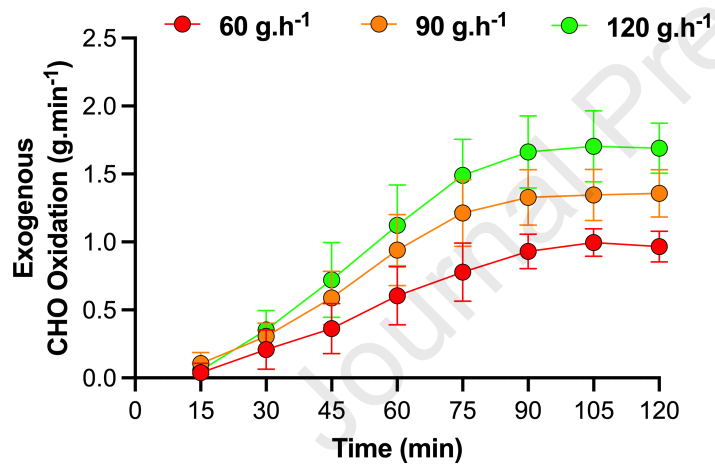
■ Semi-Solid □ Solid ▒ Fluid



(A)



(B)



(C)

