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1 **Fibre for performance horses: A review**

2

3 **Abstract**

4 Traditionally, performance horses are often fed high quantities of cereal grain-containing
5 feeds to sustain their high energy needs and consequently the forage portion of the diet is
6 reduced. Unfortunately such feeding practices are associated with adverse health effects and
7 thus some investigations into alternative feedstuffs for performance horses have been
8 undertaken. This paper reviews the ability of high energy fibrous feeds, such as haylage,
9 sugar beet pulp and soyhulls, to meet the energy and protein requirements of performance
10 horses, such as racing Thoroughbreds and Standardbred horses. Further, it explores the
11 effects of these feedstuffs on bodyweight and other parameters generally associated with
12 performance. The literature suggests that high energy fibrous feeds may have digestible
13 energy contents comparable to grain as a consequence of enhanced volatile fatty acid (VFA)
14 production. The inclusion of high energy fibrous feeds in performance horse diets does not
15 appear to adversely affect glycogen utilisation or muscle lactate clearance during intense
16 exercise, and an alkalisng effect of a haylage-only diet may offset acidosis induced by
17 intense exercise. Increases in bodyweight have been observed with haylage-only diets, but to
18 a lesser extent than those observed for hay, and this has been attributed to the water holding
19 capacity of the fibres. Whilst considerable research is required to fully understand the effects
20 of high energy fibrous feeds in the diets of performance horses and its ability to sustain their
21 nutrient requirements, the literature currently supports the replacement of at least a portion
22 the grain fraction of the daily feed ration with high energy fibrous feed products. The
23 implementation of such a change would likely improve the welfare of the performance horse.

24

25 **1. Introduction**

26 Diets of performance horses commonly consist of small quantities of low energy forage and
27 large quantities of high-starch cereal grains or concentrates [1,2,3,4,5]. This practice focuses
28 on foregut digestion aiming to capitalise on glucose delivery as a result of starch digestion in
29 the small intestine [2]. However, such feeding regimes have been associated with alterations
30 in the microbial population of the hind gut [6], disturbances of gastric function, promotion
31 of colic, and an elevated risk of laminitis [2,7,8,9]. In addition, large grain-containing meals
32 have been associated with the formation of gastric ulcers [10] and the development of
33 stereotypical behaviours [11,12]. Thus, current feeding practices for performance horses may
34 pose a welfare issue and consequently there is a need to explore alternative feeding regimens.
35 A potential solution may include reducing the quantity of high starch-containing
36 concentrates and replacing them with energy-dense fibrous feeds. This review aims to
37 consider whether energy-dense fibrous feeds are suitable alternatives to high-starch feeds for
38 performance horses.

39

40 **2. Fibre versus grains: Energy**

41

42 Grain is comprised mostly of hydrolysable carbohydrates (starch) and a small portion of
43 fibre. When grain is fed, the hydrolysable dietary carbohydrates are digested in the small
44 intestine, firstly, by alpha-amylase secreted by the pancreas, and then by brush–border
45 membrane disaccharidases (sucrose, maltase, lactase) [13]. Sucrase activity is highest in the
46 proximal portion of the small intestine, whereas maltase activity is similar throughout all
47 regions [14]. Lactase activity is also prominent in the proximal region but expression reduces
48 with maturity of the horse [14]. Following digestion of the hydrolysable carbohydrates, the

49 resulting monosaccharides (D-glucose, D-fructose, D-galactose) are then absorbed across the
50 brush-border membrane by specific monosaccharide transporters [13]. Glucose and
51 galactose are transported via Na⁺/glucose cotransporter isoform 1 (SGLT1) which is
52 expressed most highly in the proximal small intestine and whilst it has a high affinity for the
53 sugar substrates, its capacity is low [14]. Thus, starch digestion is somewhat limited by
54 physiology, with the majority of digestion and absorption of sugars occurring in the proximal
55 portion of the small intestine.

56

57 Fibrous feeds are mostly digested in the hindgut. Microbial fermentation in the hindgut
58 produces volatile fatty acids (VFA), principally acetate, propionate and butyrate. These
59 energy-yielding substrates are readily absorbed into the bloodstream and converted to
60 glucose, fat, or utilised directly as an energy source. The respective concentrations of acetate,
61 propionate and butyrate are greatly influenced by diet and this has been demonstrated by
62 numerous investigators [15,16,17,18]. For example, Julliand et al. [19] demonstrated that the
63 inclusion of barley in a hay-based diet led to significant changes in the microbial population
64 of the colon resulting in a lower colonic pH, a decreased molar percentage of acetate and an
65 increased molar percentage of propionate.

66

67 In contrast to the potentially detrimental effects of grain on hindgut dynamics and VFA
68 production, energy-dense fibrous feeds have been shown to enhance VFA production in the
69 equine hindgut, and the superior fermentation qualities of haylage, sugar beet pulp, and
70 soyhulls in comparison to hay, have been demonstrated by several investigators.

71

72 Moore-Colyer et al. [20] reported sugar beet pulp to exhibit greater fermentation potential
73 than hay cubes when fed to ponies, with sugar beet fibre yielding significantly higher levels
74 of intra-caecal VFAs (20.46mmol/kg sugar beet fibre) compared to hay cubes
75 (14.85mmol/kg hay cubes). Similarly, Coverdale et al. [17] reported Quarter Horses fed an
76 alfalfa/bromegrass hay diet, substituted with 0, 25, 50 or 75% soyhulls, to have increased
77 total caecal VFA concentration from 70.32mM to 108.50mM for 0 and 75 % soyhull
78 supplementation, respectively. Moreover, Muller [21] assessed levels of total VFAs in the
79 faeces of 12 horses fed haylage cut at 3 different stages of maturity. The early cut haylage
80 (June) was found to produce significantly greater ($p<0.05$) quantities of total faecal VFAs
81 (June 55.2mM), particularly acetate and propionate, than the later cut haylages (July
82 42.1mM; August 38.4mM).

83

84 The enhanced production of VFAs in the large intestine with the inclusion of haylage, sugar
85 beet pulp, and soyhulls in the diet has been attributed to a high concentration of readily
86 degradable non-starch polysaccharides (NSP) in these feedstuffs [20,22,23,24]. NSPs,
87 particularly arabinose, galactose, and uronic acid from the pectin fraction, are highly
88 fermentable [24,25] making these fibrous feeds potent sources of energy for the horse.

89

90 The significance of enhanced fermentation and subsequent increase in VFA production
91 becomes apparent when one considers that these substrates are converted to glucose, fat, or
92 used directly as a source of energy. The two VFAs that contribute most to energy
93 metabolism are acetate and propionate. Acetate represents approximately 70% of all VFAs
94 produced [16] and is a metabolic precursor to acetyl-CoA. Under aerobic conditions acetate
95 can be utilised via the tricarboxylic acid cycle to produce adenosine triphosphate (ATP), or

96 converted to fat [26]. Pethick et al. [27] reported acetate to account for up to 32% of the total
97 substrate oxidation within the hind limb at rest. Pratt et al. [28] also confirmed acetate's role
98 as an energy substrate, having observed an enhanced utilisation of plasma acetate following
99 an infusion of sodium acetate during sub-maximal exercise compared to rest. It is important
100 to note that haylage has been shown to positively influence plasma acetate concentration;
101 Jansson and Lindberg [29] observed a significantly higher concentration of plasma acetate in
102 Standardbred horses fed a haylage-only diet (timothy, meadow fescue mixture), before and
103 after exercise, compared to a 50:50 haylage:concentrate diet.

104

105 Propionate is a gluconeogenic substrate [30] and its contribution to the glucose pool is
106 substantial. Approximately 7% of total glucose production in ponies fed hay has been
107 reported to originate from caecal propionate [31], with 50-61% of blood glucose in ponies
108 fed hay derived from colonic propionate [32]. The remaining 32-43% of glucose is likely
109 assimilated via the small intestine or from gluconeogenesis from amino acids [32].

110

111 The aforementioned studies serve to remind us that horses are designed to efficiently extract
112 energy substrates from hindgut fermentation, if fuelled appropriately, and the old adage of
113 "keeping the fire stoked" may be applicable in this case.

114

115 In contrast to times gone by when low energy hay was the only source of conserved forage,
116 the highly digestible and fermentable nature of higher energy fibrous feeds may indeed
117 potentially enable them to replace starch as an energy source for performance horses [33,34].
118 However, empirical quantification of the digestible energy (DE) content of these higher
119 energy fibrous feeds needs further development if such feed types are to be accurately

120 incorporated into feed rations. The formulas used to estimate DE are reasonably accurate for
121 feed products including hay and most pellet feeds [35,36], but they may substantially
122 underestimate the DE for feed products containing over 35% crude fibre (eg. soyhulls) and
123 for fibrous products with a high content of highly fermentable fibres (eg. sugar beet pulp)
124 [36]. Table 1 provides details of published average DE values for a variety of fibrous
125 feedstuffs and cereal grains. According to Zeyner and Kienzle [36] it is likely the DE values
126 for sugar beet pulp and soyhulls may be more comparable to that of oats and barley.

127

128 Despite the theory supporting the inclusion of high energy fibrous feedstuffs in performance
129 horse diets, substantial debate exists over whether these alternative feedstuffs can meet the
130 energy requirements of the performance horse in practise. Performance horses, such as
131 racehorses, primarily rely on the metabolism blood glucose and muscle glycogen for energy
132 production and replenishment of glycogen stores [18,37]. As such, an abundant supply of
133 glucose to muscle is essential to prevent fatigue and reduced performance [38]. Moreover,
134 as many horses in the racing industry commence their training from a young age, the diet
135 must support growth and development, in addition to meeting the energy requirements
136 imposed by training. In support of this notion, Ringmark et al. [39] reported that yearling
137 Standardbred horses fed a forage-only diet grew as well as yearlings fed conventional diets,
138 had normal body condition and muscle glycogen levels for athletic horses, and achieved
139 conventional training goals. Thus, there is evolving evidence to suggest high energy fibrous
140 feeds may be able to adequately support these elevated requirements.

141

142 **2.1 Blood glucose**

143 In general, fibrous feeds are considered to be relatively low contributors to blood glucose

144 production compared to grain-containing meals due to their relatively low levels of
145 non-structural carbohydrates and studies examining glucose levels following a meal of
146 “fibre” versus a meal of “starch/sugars” in horses at rest have substantiated such claims
147 [40,41,42]. For example, Karasu et al. [43] reported peak glucose concentration and plasma
148 AUC glucose concentration in horses at rest following a meal comprised of a
149 “fibre-enriched” compound feed (starch 7.4g, sugar 6.2g [as fed]) was 5.2 ± 0.2 mmol/L and
150 163 ± 46 mmol x min/L, respectively. In contrast, following a meal of starch-enriched
151 compound feed (starch 33.1g, sugar 4.4g [as fed]) the peak glucose concentration and plasma
152 AUC concentration was 7.6 ± 0.9 mmol/L and 696 ± 208 mmol x min/L. Interestingly, a
153 second meal fed 8.5 hours later produced a similar glycemic response for the fibre-enriched
154 meal, but a substantially reduced glycemic response for the starch-enriched meal. Further,
155 Lindberg and Palmgren-Karlsson [44] replaced a portion of a meal containing oats with sugar
156 beet pulp (145g/kg DM oats replaced with 152g/kg DM unmolassed sugar beet pulp to
157 produce a diet containing 179g/kg DM starch and 106g/kg DM starch, respectively). Blood
158 glucose levels were observed over a 4 hour period. At 2 hours post-meal blood glucose levels
159 peaked at 7.5 mmol/L for the oats diet and were significantly higher than for the sugar beet
160 pulp diet (6.8 mmol/L). However, by 4 hours post-meal blood glucose levels for both diets
161 were equivalent.

162

163 In contrast, Crandell, et al. [45] reported that post-feeding blood glucose levels in horses fed
164 a diet of sweet feed (cereal concentrate) compared to when 15% of the daily digestible energy
165 intake was replaced with molassed sugar beet pulp (1.36kg dry weight) were similar, but a
166 contribution to the blood glucose levels by molasses to the sugar beet pulp cannot be ruled
167 out. Likewise, Groff et al. [46] observed that horses fed 0.75kg of molassed sugar beet pulp

168 produced statistically similar peak blood glucose concentration, mean glucose concentration
169 and area under the curve responses compared to an equal weight of whole oats. However, it
170 was also noted that this parity in peak blood glucose concentration was most likely due to the
171 inclusion of molasses in the sugar beet pulp, as observed by Crandell et al. [45]. However,
172 unmolassed sugar beet pulp also elicited a blood glucose peak during the first 150 minutes
173 post-ingestion. This effect was reportedly due to the digestion of residual sugars [46], but
174 may also have been due to enzymatic digestion of non-starch polysaccharides (NSP) in the
175 small intestine. Moore-Colyer et al. [24] reported that 15% of sugar beet pulp NSPs and
176 14% of soyhull NSPs disappeared pre-caecally in ponies.

177

178 Considering the digestion process of high energy fibrous feeds, it may be more appropriate to
179 assess blood glucose levels over a longer time period and consider area under the curve
180 concentrations in addition to peak blood glucose levels. Groff et al. [46] reported that whilst
181 horses fed 0.75 kg of unmolassed sugar beet pulp exhibited lower peak blood glucose
182 concentrations compared to a meal of 0.75kg whole oats, they produced statistically similar
183 mean glucose concentrations and area under the curve concentrations. This is due to higher
184 concentrations of blood glucose 150-480 minutes post-ingestion of unmolassed sugar beet
185 pulp compared to the whole oats. A similar observation was made by Hallebeek and Beynen
186 [47] who reported that 3 hours after ingestion of a base diet (grass hay and concentrate)
187 supplemented with 0.375kg unmolassed sugar beet pulp, plasma glucose and insulin
188 concentrations were significantly higher than when horses were fed the same base diet
189 supplemented with 0.215kg glucose. The apparent delay in glucose production is
190 hypothesised to be attributed to increased production and absorption of propionate from the
191 fermentation of pectins in the hindgut [33].

192

193 The enhancement of propionate production by high energy fibrous feeds may translate to a
194 greater potential for gluconeogenesis [17] specifically during performance. In contrast to
195 cereal grain which is primarily digested in the small intestine, performance horses fed higher
196 energy fibrous feeds may benefit from glucose produced via efficient enzymatic NSP
197 digestion in the small intestine, in addition to a constant supply of gluconeogenic substrates
198 from hindgut fermentation.

199

200 Thus, when examining the effects of high energy fibrous feeds on performance horse blood
201 glucose levels it is pertinent to examine their effects during and post exercise, as this may
202 have a direct affect on performance and recovery. Crandell et al. [45] reported statistically
203 similar blood glucose levels for Thoroughbred horses undergoing an intensive standard
204 exercise test when fed a diet of sweet feed (cereal concentrate) compared to when 15% of the
205 daily digestible energy intake was replaced with molassed sugar beet pulp. During the warm
206 down and 15 minute post-exercise time point, blood glucose levels were statistically higher
207 when fed the sweet feed, but this may also have been due to significantly higher cortisol
208 levels. Similarly, Palmgren Karlsson et al. [48] reported that when fed an oat/hay/molassed
209 sugar beet pulp diet (equivalent to 2.08kg oats, 1.48kg molassed sugar beet pulp for 500kg
210 horse) compared to an oat/hay diet (equivalent to 3.55kg for 500kg horse) the blood glucose
211 level of Standardbred horses during or following an intensive treadmill exercise test were
212 comparable. Similar observations in plasma glucose levels were reported by Gurbuz and
213 Coskun [49] when Thoroughbred horses undergoing an intensive exercise test were fed
214 either an oats-containing diet or the same diet with oats replaced by 12.5%, 25% and 37.5%
215 of dried sugar beet pulp.

216 These studies confirm that whilst resting blood glucose levels may be lower when fed a high
217 fibre diet compared to when fed a high-starch containing meal, blood glucose levels during
218 and immediately following exercise are equivalent and during the exercise tests no
219 detrimental effects on performance were observed.

220

221 **2.2 Glycogen utilisation**

222 During exercise both aerobic and anaerobic metabolic pathways are in operation. However,
223 depending on the intensity and duration of the exercise, one energy metabolic pathway will
224 predominate. At high speeds over short distances the rate of glycogen utilisation is at its
225 fastest due to the high activity of anaerobic energy metabolism. Any impairment to the rate of
226 glycogen utilisation during intense exercise may affect performance, and thus the effect of
227 diet on the rate of glycogen depletion is an important consideration.

228

229 Jansson and Lindberg [29] reported that following an intense exercise test, Standardbred
230 horses fed a grass haylage-only diet, versus a diet containing 50:50 concentrate:haylage,
231 experienced similar glycogen depletion rates and performance was not affected. This
232 suggests that the haylage-only diet was able to provide sufficient energy substrates to
233 produce performance equivalent to a starch-containing diet with no adverse effects on
234 glycogen utilisation. Similarly, Essen-Gustavsson et al. [50] reported no difference in rate of
235 glycogen utilisation when horses undergoing an intense exercise test were fed a forage-only
236 diet (silage/hay) containing high levels of crude protein (16.6%) versus a recommended level
237 of crude protein (12.5%).

238

239 Palmgren Karlsson et al. [48] suggested that the inclusion of sugar beet pulp in performance
240 horse diets may also yield positive effects on glycogen utilisation. They observed
241 significantly higher muscle glycogen concentrations ($p < 0.05$), significantly lower muscle
242 lactate levels ($p < 0.05$) and significantly lower peak plasma lactate concentrations (during
243 Phase I ($p < 0.0001$) and Phase III ($p < 0.05$) of an exercise test) in Standardbred horses
244 following an intensive treadmill exercise test when they were fed an oat/hay/sugar beet pulp
245 diet compared to an oat/hay diet. Palmgren Karlsson et al. [48] proposed that the additional
246 VFAs, produced as a result of the sugar beet pulp, were utilised as an aerobic energy
247 substrate creating a glycogen-sparing effect. Whilst it is important to consider that these
248 results may have been influenced by the presence of molasses in the diet containing sugar
249 beet pulp, their findings display similarities consistent with findings observed by Jansson and
250 Lindberg [29] with regards to lower plasma lactate concentrations and a trend towards higher
251 aerobic energy metabolism in horses fed a haylage-only diet. However, a repeat of this
252 experiment with unmolassed sugar beet pulp would help to clarify if glycogen-sparing does
253 occur.

254

255 Based on the limited available research, the inclusion of grass haylage or sugar beet pulp in
256 performance horse diets does not appear to adversely affect the rate of glycogen utilisation.
257 Pending further research, it is possible that the inclusion of sugar beet pulp may exhibit a
258 glycogen-sparing effect. Moreover, it would be valuable to explore the effects of soyhulls
259 on glycogen utilisation and due to its highly fermentative properties it may be possible to
260 draw some parallels with sugar beet pulp.

261

262 **2.3 Glycogen replenishment**

263 As glycogen is a limiting fuel for muscle contraction and reduced glycogen stores have been
264 shown to impair subsequent performance [35,51], it is important that any diet must
265 adequately facilitate glycogenesis. In humans, dietary manipulation of carbohydrates to
266 enhance muscle glycogen stores and hasten repletion to gain a competitive advantage has
267 been extensively researched [52]. Similar research has been conducted in horses; however,
268 unlike humans, the process of glycogen replenishment in the horse appears to be
269 physiologically rate limited. Feeding diets containing high levels of non-structural
270 carbohydrates (starch, glucose) have been unsuccessful at substantially hastening the
271 repletion process to less than 48-72 hours [53,54,55]. For example, Snow and Harris [53]
272 investigated glycogen repletion rates in trained Thoroughbred horses subjected to a typical
273 British training exercise programme. Following exercise, muscle glycogen loss was between
274 19-25% of the resting content. Horses received ~3.5kg hay and ~7kg concentrate feed
275 providing 38.5% dietary starch per day. Despite the high levels of starch it still took 72 hours
276 for glycogen levels to return to pre-exercise levels. Lacombe et al. [56] reported that only a
277 grain diet containing very high levels of starch (51%) was able to replenish muscle glycogen
278 stores in Standardbred horses depleted to 60% of baseline values within 72 hours. As the
279 average glycogen depletion rate for racehorses is generally accepted to be around 20-35% of
280 baseline levels due to the short duration of the intense exercise [57,58,59] providing such
281 high levels of starch is not recommended due to potential adverse health effects.

282

283 Concern over whether all forage diets can sustain adequate glycogen reserves was
284 highlighted when Jansson and Lindberg [29] reported significantly lower ($p < 0.05$) pre- and

285 post-exercise muscle glycogen levels (-13%) in Standardbred horses consuming an early-cut
286 haylage-only diet (pre-exercise 560 ± 22 mmol glucosyl units/kg dry weight (DW);
287 post-exercise 473 ± 22 mmol/kg DW) compared to a 50:50 haylage:concentrate diet
288 (pre-exercise 644 ± 22 mmol/kg DW; post-exercise 546 ± 22 mmol/kg DW). The authors
289 speculated that the difference in muscle glycogen levels may have been due to the horses
290 being exercised 96 hours prior to the standardised exercise test and it was postulated that
291 glycogen repletion may not have been complete for the haylage-only diet. However, Jansson
292 and Lindberg [29] also considered that the low crude protein content of the haylage-only diet
293 (~10% CP) may have influenced glycogen repletion as described by Essen-Gustavsson et al.
294 [50].

295

296 Essen-Gustavsson et al. [50] reported that horses fed a forage-only diet (silage/hay)
297 containing high levels of crude protein (CP) (16.6%) had higher levels of muscle glycogen at
298 rest (pre-exercise), post-exercise and after 90 minutes of recovery than when fed a
299 forage-only diet containing “recommended” levels for racehorses of CP (12.5%).
300 Pre-exercise muscle glycogen levels were reported to be 630 mmol/kg dry weight (DW) for
301 the high protein diet and 552 mmol/kg DW for the recommended protein diet, which
302 incidentally are comparable to the pre-exercise values observed by Jansson and Lindberg
303 [29] in horses fed a 50:50 forage:concentrate diet (644 ± 22 mmol/kg DW) and a forage-only
304 diet (560 ± 22 mmol /kg DW). Essen-Gustavsson et al. [50] proposed that the increase in
305 muscle glycogen concentration for the high protein group was related to either a greater
306 synthesis of muscle glycogen or a lower degradation rate of muscle glycogen [50].
307 However, it is of note that the diets were not isocaloric, with the HP diet containing
308 significantly higher metabolisable energy. Also the water soluble carbohydrate intake was

309 300g higher on the high protein diet but this difference in water soluble carbohydrates was
310 not believed by the authors to be substantial enough to affect glycogen synthesis.

311

312 Studies in humans have shown that an intake of carbohydrates plus protein is more effective
313 at replenishing glycogen than carbohydrates alone (Zawadski et al., 1992 cited by [50]; Van
314 Loon et al., 2000 cited by [50]). The mechanism is not completely understood but may be
315 related to the stimulation of insulin secretion by amino acids (leucine, iso-leucine) leading to
316 increased uptake of glucose by skeletal muscles [50]. Furthermore, in rats it is thought that
317 muscle glycogen synthesis may be stimulated by leucine activating the mTOR (mammalian
318 Target of Rapamycin) signal pathway ultimately leading to the stimulation of glycogen
319 synthase and production of glycogen (Morifuji et al., 2010 cited by [50]). Morifuji et al. [60]
320 also demonstrated in rats that feeding a carbohydrate meal combined with a protein
321 hydrolysate pre-exercise attenuated exercise induced glycogen depletion. Interestingly, it
322 was noted by Essen-Gustavsson et al. [50] that the muscle leucine concentration in muscle
323 was higher in the high protein diet post-exercise compared to the recommended protein diet
324 fed to horses. Research exploring the effect of high protein haylage combined with sugar beet
325 pulp as a supply of fibre and sugars on muscle glycogen levels would be interesting.

326

327 Pending further research regarding the ability of high energy fibrous feeds to efficiently
328 replenish glycogen supplies it may be prudent to include a limited source of sugar/starch in
329 equine diets following strenuous exercise, particularly if further strenuous exercise is
330 expected to occur within a few days.

331

332 **3 . Fibre versus grains: performance**

333 Several factors may influence the athletic performance of the equine. These include
334 accumulation of by-products from energy metabolism (lactate), perceived effects of
335 excessive dietary protein, and increased bodyweight/gut-fill. Several studies have examined
336 the effects of high-energy fibrous feeds on these factors.

337

338 **3.1 Muscle lactate and H⁺ clearance**

339 High intensity exercise in the equine athlete can result in marked accumulation of muscle
340 lactate and hydrogen ions (H⁺) [58], and excessive intra-muscular accumulation of lactate
341 and H⁺ can lead to intracellular acidosis resulting in fatigue [61,62]. The monocarboxylate
342 transporter isoform 4 (MCT4) is found in glycolytic muscle fibres, and is believed to be
343 specialised for lactate efflux [63]. MCT4 expression has been shown to be increased by
344 induced alkalosis enhancing lactate and H⁺ clearance from glycolytic muscles [64]. The
345 resultant plasma lactate and H⁺ may then be taken up by MCT1 in oxidative muscle fibres for
346 conversion to pyruvate [65]. Therefore, strategies to enhance muscle lactate and H⁺ clearance
347 via induced alkalosis have been explored [66,67]. Administration of a bicarbonate solution to
348 horses is an example of a commonly used method to induce alkalosis [68]. A serendipitous
349 side effect of a haylage-only diet may be to facilitate muscle lactate and H⁺ clearance via a
350 natural alkalisating effect. Jansson and Lindberg [29] reported that Standardbred horses
351 undergoing an intensive standard exercise test and fed early cut grass haylage-only diets, had
352 significantly higher venous blood pH levels (p<0.05) at several testing points compared to
353 when fed the 50:50 early-cut grass haylage:concentrate diet. The haylage-only fed horses
354 also had significantly lower plasma lactate concentration post-exercise (p<0.05) and trended
355 towards a higher plasma lactate threshold (V_{La4}) (p=0.086). Jansson and Lindberg [29]

356 proposed that the lower plasma lactate concentration post-exercise test may have been due to
357 a reduced dependency upon glycolytic metabolism and increased aerobic metabolism.
358 However, as the rate of glycogen depletion between the two diets was similar it could be
359 speculated that the lower plasma lactate levels may be a result of greater uptake by MCT1.
360 This may be a consequence of enhanced muscle lactate clearance due to greater MCT4
361 expression as a result of the alkalisising effect of the haylage-only diet. Additionally, the more
362 alkaline blood pH may have been due to the buffering capacity (organic anions) of the
363 haylage-only diet neutralising H⁺ ions [29]. This is certainly an interesting area warranting
364 further investigation. The capacity to offset acidosis induced by intense exercise, via natural
365 means, may be a real benefit to the performance horse.

366

367 **3.2 High protein forage and performance**

368 The CP content of many fibrous feeds is often equivalent to, or in excess of, that found in
369 cereal grains [69]. The average CP content of sugar beet pulp, haylage and soyhulls is 10%,
370 13% and 14% respectively, which is less than or comparable to cereal grain (12-13%) [35].
371 However, legume forages tend to have a higher CP content, often exceeding 20% of the DM
372 content [35]. This may be of concern to some in the performance industry as the effect of
373 high dietary protein levels on performance has been scrutinised over the years. Glade [70]
374 reported that CP intakes were positively correlated with racehorse time to finish with
375 ingestion of over 1630g CP/day/500kg bodyweight, increasing average “times to finish” by
376 1-3 seconds. Moreover, Connysson et al. [69] reported that excretion of excess protein
377 produces hydrogen ions that may potentially affect the horse’s acid-base balance, and the
378 heat produced during excretion along with the increased urinary output contributes to
379 evaporative fluid loss. They suggested that together these factors may potentially provide

380 horses with unnecessary challenges during “prolonged” exercise.

381

382 Nonetheless, under experimental conditions, adverse effects of high levels of protein intake
383 on performance are yet to be substantiated. Miller-Graber et al. [71] did not observe
384 increased sweat loss in 6 conditioned Quarter Horse mares fed a high protein diet (18% CP)
385 during an intense, sub-maximal exercise test when compared to a low protein diet (9.0% CP).
386 Similarly, Jansson and Lindberg [29] reported that 6 Standardbred geldings in race training
387 fed haylage-only (1132 ± 87 g CP) or 50:50 haylage:concentrate (1467 ± 66 g CP) diets did
388 not show differences between diets for heart rate, breathing frequency or rectal temperature
389 before, during or after an intensive treadmill exercise test. Essen-Gustavsson et al. [50] also
390 did not report any adverse effects of a forage-only diet (16.6% CP) on the metabolic response
391 of horses during an exercise test. Thus, the effect of excessive levels of dietary CP on
392 performance needs further investigation and it would appear from the literature that there are
393 few adverse effects on performance. Thus the inclusion of legume forages or haylage in
394 moderation in performance horse diets should not be discouraged.

395

396 **3.3 Bodyweight and performance**

397 Weight and gut-fill are a major concern for performance horses as “dead weight” may confer
398 a real handicap. The increased bodyweight may increase the overall workload of the horses,
399 ultimately impairing performance [72]. Forages, particularly hay, are provided in limited
400 quantities to prevent potential bodyweight increases [73] created by the extra dry matter and
401 the water holding capacity of fibres [72]. Additionally, extra gut fill and weight may impact
402 on the energy expenditure of a hard working horse. Kronfeld [74] proposed that 5.6% extra
403 weight in a 500kg horse due to additional fibre and water would increase energy expenditure

404 by 1.8Mcal/day.

405

406 Certainly increases in bodyweight have been observed when horses are fed all-hay or diets
407 with large quantities of hay. Ellis et al. [73] showed that Thoroughbred-type geldings fed
408 late-cut meadow hay (full bloom stage) as either 100% hay, 80% hay:20% concentrate, 60%
409 hay:40% concentrate or 50% hay:50% concentrate experienced significant changes in
410 bodyweight. Over the course of the study the mean bodyweight of horses on the 100% hay
411 diet increased approximately 7kg (1.3% increase), and the 80% hay diet increased weight by
412 approximately 3kg (0.5% increase). In contrast, the 60% hay diet decreased bodyweight by
413 approximately 5kg (0.9% decrease), and the 50% hay diet decreased approximately 4kg
414 (0.7% decrease). Water consumption was also greatest when horses were consuming the
415 100% hay diet (45 l/d) and was statistically greater than when consuming the 50% hay:50%
416 concentrate diet (39 l/d). The increased bodyweight in the higher forage diets was attributed
417 to increased dry matter intake, increased water intake and slower rate of passage of digesta
418 leading to greater gut fill. Following a sub-maximal standard exercise test maximal heart rate
419 and recovery heart rate were significantly higher when horses were fed the 100% hay diet
420 compared to the 50% hay:50% concentrate diet. Ellis et al. [73] concluded that the
421 increased bodyweight may have contributed to the increased heart rates and this may be
422 detrimental to the performance of the horse.

423

424 In contrast to low energy fibres, such as hay, the high energy fibres being of higher calorific
425 content, are fed in lower quantities than hay, and thus are expected to have a smaller impact
426 on gut fill and body weight. Meyer [75] published findings of the effects of meadow hay and
427 mixed feeds on gut fill in exercised horses. It is possible a diet comprised of a high energy

428 haylage and a pelleted high energy fibre concentrate may have a similar or potentially lower
429 gut fill (g/kg bwt) than reported for the exercised horses fed meadow hay and mixed feed [75]
430 thus not rendering performance horses consuming high energy fibrous feeds diets at a
431 disadvantage.

432

433 Limited research has been conducted exploring the effects of high energy fibrous feeds on
434 bodyweight. Jansson and Lindberg [72] reported weight gain in horses fed haylage but to a
435 lesser extent than reported by Ellis et al. [73] when hay was fed. Standardbred horses
436 undergoing intense track work fed a haylage-only diet had a small (3-5kg) weight gain
437 compared to the 50:50 haylage:concentrate diet [72]. However, almost all of the additional
438 weight gain was lost during a period of feed deprivation (time between last forage meal
439 [afternoon prior to exercise test] and just prior to warm up for exercise test) suggesting the
440 majority of extra weight was due to feed bulk and water retention [72]. Despite the slight
441 increase in weight performance was not adversely affected during the intensive exercise test.
442 No impact was observed for breathing frequency, heart rate or general performance [72].
443 Further, Spooner et al. [76] observed that endurance horses completing a 60km exercise test
444 trended towards greater body mass loss when fed a 50:50 grass hay:soyhull/sugar beet
445 pulp/oil-supplemented diet compared to a grass hay-alone diet or 50:50 grass hay:alfalfa diet
446 ($p=0.08$). This difference was speculated to be due to greater faecal water loss over the
447 exercise test period [76].

448

449 The research suggests that diets containing high energy fibrous feeds may increase
450 bodyweight due to their increased water holding capacity but this weight gain is less than that
451 observed for diets comprised of hay alone. Strategic feeding and a short period of dietary

452 restriction prior to competition may facilitate loss of additional weight. However, further
453 research in this area is needed, particularly for sugar beet pulp and soyhulls, as their highly
454 digestible properties may equate to less gut-fill, and hence, less “dead weight”.

455

456 **5. Conclusion**

457 There is strong evidence to support the need for alternative feeding practices for performance
458 horses due to the adverse health effects associated with high-starch diets, and high energy
459 fibrous feeds may go some way to providing a solution.

460

461 A review of the literature suggests that during and following exercise blood glucose levels
462 are equivalent to when horses are fed starch-containing diets, and the rate of glycogen
463 utilisation is not adversely affected by diets containing haylage or sugar beet pulp. In fact,
464 sugar beet pulp may offer a glycogen-sparing effect due to the enhanced production of
465 propionate and its gluconeogenic properties. Optimal strategies for facilitating efficient
466 glycogen replenishment are still being investigated and a starch-containing meal following
467 glycogen repletion may be necessary if periods between performances are short. High CP
468 levels, such as those found forages such as alfalfa, may have a positive effect on glycogen
469 synthesis.

470

471 Regarding performance parameters, the inclusion of high energy fibrous products (haylage,
472 sugar beet pulp) in performance horse diets does not appear to adversely affect muscle lactate
473 clearance. Moreover, an alkalising effect of a haylage-only diet may offset acidosis induced
474 by intense exercise and promote muscle lactate clearance. Additionally, under experimental
475 conditions high CP diets have not been shown to adversely affect performance. Weight and

476 gut-fill may be less of an issue for high energy fibrous feeds such as haylage, sugar beet pulp,
477 and soyhulls as they are more digestible across the total digestive tract than hay.

478

479 Whilst considerable research is required to fully understand the effects of the high energy
480 fibrous feeds in the diets of performance horses, the present literature presents a sound
481 argument for the replacement of at least some of the grain with high energy fibrous feeds.

482 This change in feeding management would substantially improve the welfare of the
483 performance horse.

484

485 **Table 1:** Average digestible energy content for grass haylage, Lucerne haylage, sugar beet pulp,
486 soyhulls, Controlled Fermented Lucerne, oats and barley.

487

Feed product	Dietary Energy (Mcal/kg DM)	Reference
Grass haylage - Early cut Timothy/Meadow Fescue	2.96	[21]
Lucerne haylage	2.93	[77]
Sugar beet Pulp	2.64-3.10	[35,78]
Soyhulls	2.04 – 2.25	[35,78]
Controlled Fermented Lucerne	2.65 (as fed)	[79]
Oats	3.23 - 3.35	[35,78]
Barley	3.64 – 3.67	[35,78]

488

489 **References**

- 490 [1] Southwood LL, Evans DL, Hodgson DR, Bryden WL, Reuben JR. The effect of roughage
491 source on exercise performance and metabolism in Thoroughbred horses. *Cornell Vet*
492 1993;83:243-55.
- 493 [2] Richards N, Hinch GN, Rowe JB. The effect of current grain feeding practices on hindgut
494 starch fermentation and acidosis in the Australian racing Thoroughbred. *Aust Vet J*
495 2006;84(11):402-7.
- 496 [3] Demirel G. Feeding practices for racehorses in Turkey. *Istanbul Universitesi Veteriner*
497 *Fakultesi Dergisi* 2006;32(2):79-86. Available at:
498 <https://journals.istanbul.edu.tr/tr/index.php/veteriner/article/view/19316/18424>. Last
499 accessed 10th October 2013.
- 500 [4] Williamson A, Rogers CW, Firth EC. A survey of feeding, management and faecal pH of
501 Thoroughbred racehorses in the North Island of New Zealand. *New Zeal Vet J*
502 2007;55(6):337-41.
- 503 [5] Burk AO, Williams CA. Feeding management practices and supplement use in top-level
504 event horses. *Comp Exerc Physiol* 2008;5(2):85-93.
- 505 [6] De Fombelle A, Varloud M, Goachet A-G, Jacotot E, Philippeau C, Drogoul C, Julliand
506 V. Characterization of the microbial and biochemical profile of the different segments of the
507 digestive tract in horses given two distinct diets. *Anim Sci* 2003;77:293-304.
- 508 [7] Davidson N, Harris P. Nutrition and welfare. In: Waran N, editor. *The Welfare of Horses,*
509 *The Netherlands: Springer; 2007, p. 45-76.*
- 510 [8] Hill, J. Impacts of nutritional technology on feeds offered to horses: A review of effects of
511 processing on voluntary intake, digesta characteristics and feed utilisation. *Anim Feed Sci*
512 *Tech* 2007;138:92-117. Available at: <http://dx.doi.org/10.1016/j.anifeedsci.2007.06.018>
513 Last accessed 23rd April 2012.

- 514 [9] Willing B, Voros A, Roos S, Jones C, Jansson A, Lindberg JE. Changes in faecal bacteria
515 associated with concentrate and forage-only diets fed to horses in training. *Equine Vet J*
516 2009;41(9):908-14.
- 517 [10] Murray MJ, Schusser GF, Pipers FS, Gross SJ. Factors associated with gastric lesions in
518 Thoroughbred horses. *Equine Vet J* 1996;28(5):368-74.
- 519 [11] Nicol CJ. Stereotypies and their relation to management. In: Harris PA, Gomarsall G,
520 Davidson HPB, Green R, editors. *Proceedings of the BEVA Specialist Meeting on Nutrition*
521 *and Behaviour*. Newmarket: Equine Veterinary Journal Ltd; 1999, p. 11-14.
- 522 [12] Waters AJ, Nicol CJ, French NP. Factors influencing the development of stereotypic
523 and redirected behaviours in young horses: findings of a four year prospective
524 epidemiological study. *Equine Vet J* 2002;34(6):572-9.
- 525 [13] Ellis AD, Hill J. *Nutritional Physiology of the Horse*. Nottingham: Nottingham
526 University Press; 2005.
- 527 [14] Dyer J, Fernandez-Castano Merediz E, Salmon KSH, Proudman CJ, Edwards GG,
528 Shirazi-Beechey SP. Molecular characterisation of carbohydrate digestion and absorption in
529 equine small intestine. *Equine Vet J* 2002;34(4):349-58.
- 530 [15] Hintz HF, Argenzio RA, Schryver HF. Digestion coefficients, blood glucose levels and
531 molar percentage of volatile fatty acids in intestinal fluid of ponies fed varying forage-grain
532 ratios. *J Anim Sci* 1971;33(5):992-5.
- 533 [16] Glinsky MJ, Smith RM, Spires HR, Davis CL. Measurement of volatile fatty acid
534 production rates in the cecum of the pony. *J Anim Sci* 1976;42:1465-70. Available at:
535 <http://www.journalofanimalscience.org/content/42/6/1465>. Last accessed 29th August 2013.
- 536 [17] Coverdale JA, Moore JA, Tyler HD, Miller-Auwerda PA. Soybean hulls as an
537 alternative feed for horses. *J Anim Sci* 2004;82:1663-68.
- 538 [18] Pratt-Phillips SE, Lawrence LM. Nutrition of the Performance Horse. In: Hodgson DR,
539 Harrington McKeever K, McGowan CM, editors. *The Athletic Horse*. 2nd ed, St Louis:
540 Elsevier; 2014, p. 34-55.

- 541 [19] Julliand V, de Fombelle A, Drogoul C, Jacotot E. Feeding and microbial disorders in
542 horses: Part 3 – Effects of three hay:grain ratios on microbial profile and activities. J Equine
543 Vet Sci 2001;21(11):543-6. Available at:
544 [http://dx.doi.org/10.1016/S0737-0806\(01\)70159-1](http://dx.doi.org/10.1016/S0737-0806(01)70159-1). Last accessed 11th December 2015.
- 545 [20] Moore-Colyer MJS, Longland AC. Intakes and *in vivo* apparent digestibilities of four
546 types of conserved grass forage by ponies. Anim Sci 2000;71:527-34.
- 547 [21] Muller CE. Equine digestion of diets based on haylage harvested at different plant
548 maturities. Anim Feed Sci Tech 2012;177:65-74. Available at:
549 <http://dx.doi.org/10.1016/j.anifeedsci.2012.06.002>. Last accessed 5th August 2013.
- 550 [22] Quicke GV, Bentley OG, Scott HW, Johnson RR, Moxon AL. Digestibility of soybean
551 hulls and flakes and the *in vitro* digestibility of the cellulose in various milling by-products. J
552 Dairy Sci 1959;42:185-86.
- 553 [23] Bach Knudsen KE. Carbohydrate and lignin contents of plant materials used in animal
554 feeding. Anim Feed Sci Tech 1997;67:319-38. Available at:
555 [http://dx.doi.org/10.1016/S0377-8401\(97\)00009-6](http://dx.doi.org/10.1016/S0377-8401(97)00009-6). Last accessed 21st August 2013.
- 556 [24] Moore-Colyer MJS, Hyslop JJ, Longland AC, Cuddeford D. The mobile bag technique
557 as a method for determining the degradation of four botanically diverse feedstuffs in the
558 small intestine and total digestive tract of ponies. Brit J Nutr 2002;88:729-40.
- 559 [25] Murray JMD, Longland A, Hastie PM, Moore-Colyer M, Dunnett C. The nutritive value
560 of sugar beet pulp-substituted lucerne for equids. Anim Feed Sci Tech 2008;140:110-24.
- 561 [26] Votion D-M, Navet R, Lacombe VA, Sluse F, Essen-Gustavsson B, Hinchcliff KW, et
562 al. Muscle energetics in exercising horses. Equine Comp Exerc Physiol 2008;4(3/4):105-18.
- 563 [27] Pethick DW, Rose RJ, Bryden WL, Gooden JM. Nutrient utilisation by the hindlimb of
564 Thoroughbred horses at rest. Equine Vet J 1993;25(1):41-4. Available at:
565 <http://dx.doi.org/10.1111/j.2042-3306.1993.tb02899.x>. Last accessed 29th August 2013.

- 566 [28] Pratt SE, Lawrence LM, Warren LK, Powell DM. The effect of exercise on the clearance
567 of infused acetate in the horse. *J Equine Vet Sci* 2005;25(6):266-71. Available at:
568 <http://dx.doi.org/10.1016/j.jevs.2005.05.008>. Last accessed 29th August 2013.
- 569 [29] Jansson A, Lindberg JE. A forage-only diet alters the metabolic response of horses in
570 training. *Animal* 2012;6(12):1939-46.
- 571 [30] Kasumov T, Cendrowski AV, David F, Jobbins KA, Anderson VE, Brunengraber H.
572 Mass isotopomer study of anaplerosis from propionate in the perfused rat heart. *Arch*
573 *Biochem Biophys* 2007;463:110-7. Available at:
574 <http://dx.doi.org/10.1016/j.abb.2007.02.022>. Last accessed 29th August 2013.
- 575 [31] Ford EJH, Simmons HA. Gluconeogenesis from caecal propionate in the horse. *Brit J*
576 *Nutr* 1985;53:55-60.
- 577 [32] Simmons HA, Ford EJH. Gluconeogenesis from propionate produced in the colon of the
578 horse. *Brit Vet J* 1991;147(4):340-5.
- 579 [33] Brokner C, Bach Knudsen KE, Karaman I, Eybye KL, Tauson AH. Chemical and
580 physicochemical characterisation of various horse feed ingredients. *Anim Feed Sci Tech*
581 2012;177:86-97. Available at: <http://dx.doi.org/10.1016/j.anifeedsci.2012.06.005>. Last
582 accessed 9th August 2013.
- 583 [34] Nielsen BD. Practical considerations for feeding racehorses. In: Geor RJ, Harris PA,
584 Coenen M, editors. *Equine Applied and Clinical Nutrition: Health, Welfare and*
585 *Performance*. Edinburgh: Saunders Elsevier Ltd; 2013. Available at:
586 <http://dx.doi.org/10.1016/B978-0-7020-3422-0.00013-4>. Last accessed 5th August 2013.
- 587 [35] National Research Council. *Nutrient requirements of horses*. 6th ed. Washington DC:
588 The National Academies Press; 2007.
- 589 [36] Zeyner, A, Kienzle, E. (2002) A method to estimate digestible energy in horse feed. *J*
590 *Nutr* 2002;132:1771S-3S.
- 591 [37] McMiken DF. An energetic basis of equine performance. *Equine Vet J*
592 1983;15(2):123-33.

- 593 [38] Lindberg JE, Jansson A. Preventing problems whilst maximising performance. In: Ellis
594 AD, Longland AC, Coenen M, Miraglia N, editors. The impact of nutrition on the health and
595 welfare of horses, The Netherlands: Wageningen Academic Publishers; 2010, p. 299-307.
- 596 [39] Ringmark S, Roepstorff L, Essen-Gustavsson B, Revold T, Lindholm A, Hedenstrom U,
597 et al. Growth, training response and health in Standardbred yearlings fed a forage-only diet.
598 *Animal* 2013;7(5):746-53. Available at: <http://dx.doi.org/10.1017/S1751731112002261>.
599 Last accessed 9th August 2013.
- 600 [40] Williams CA, Kronfeld DS, Staniar WB, Harris PA. Plasma glucose and insulin
601 responses of Thoroughbred mares fed a meal high in starch and sugar or fat and fiber. *J Anim*
602 *Sci* 2001;79:2196-201.
- 603 [41] Treiber KH, Geor RJ, Boston RC, Hess TM, Harris PA, Kronfeld DS. Dietary energy
604 source affects glucose kinetics in trained Arabian geldings at rest and during endurance
605 exercise. *J Nutr* 2008;138:964-70.
- 606 [42] Vervuert I, Voigt K, Hollands T, Cuddeford D, Coenen M. Effect of feeding increasing
607 quantities of starch on glycaemic and insulinaemic responses in healthy horses. *Vet J*
608 2009;182:67-72.
- 609 [43] Karasu GK, Krabbenborg R, Einspanier A, Vervuert I. Insulinaemic and glycaemic
610 responses to a second meal of a fibre- or starch-enriched compound feed in healthy horses.
611 *Vet J* 2015;204:220-2.
- 612 [44] Lindberg JE, Palmgren Karlsson C. Effect of partial replacement of oats with sugar beet
613 pulp and maize oil on nutrient utilisation in horses. *Equine Vet J* 2001;33(6):585-90.
- 614 [45] Crandell KG, Pagan JD, Harris P, Duren SE. A comparison of grain, oil and beet pulp as
615 energy sources for the exercised horse. *Equine Vet J* 1999;S30:485-89.
- 616 [46] Groff L, Pagan J, Hoekstra K, Gardner S, Rice O, Roose K, et al. Effect of preparation
617 method on the glycemic response to ingestion of beet pulp in Thoroughbred racehorses. In:
618 Proceedings of the 17th Equine Nutrition and Physiology Symposium, Kentucky, U.S.A., 31
619 May – 2 June, 2001, Equine Nutrition and Physiology Society; 2001, p. 125-6.

- 620 [47] Hallebeek JM, Beynen AC. Influence of dietary beetpulp on the plasma level of
621 triacylglycerols in horses. *J Anim Physiol An N* 2003;87:181–7. Available at:
622 <http://dx.doi.org/10.1046/j.1439-0396.2003.00394.x>. Last accessed 14th August 2013.
- 623 [48] Palmgren Karlsson C, Jansson A, Essen-Gustavsson B, Lindberg JE. Effect of molassed
624 sugar beet pulp on nutrient utilisation and metabolic parameters during exercise. *Equine Vet*
625 *J* 2002;S34:44-9.
- 626 [49] Gurbuz E, Coskun B. Effect of dried sugar beet pulp on some blood parameters and
627 heart rate in exercised horses. *Kafkas Universities Veteriner Fakultesi Dergisi* [online]
628 2011;17(2):191-5. Available at: <http://vetdergi.kafkas.edu.tr>. Last accessed 9th August 2013.
- 629 [50] Essen-Gustavsson B, Connysson M, Jansson A. Effects of crude protein intake from
630 forage-only diets on muscle amino acids and glycogen levels in horses in training. *Equine*
631 *Vet J* 2010;42(S38):341-6.
- 632 [51] Lacombe VA, Hinchcliff KW, Geor RJ, Baskin CR. Muscle glycogen depletion and
633 subsequent replenishment affect anaerobic capacity of horses. *J Appl Physiol*
634 2001;91(4):1782-90. Available at:
635 <http://jap.physiology.org.ezproxy.is.ed.uk/content/91/4/1782.full.pdf+html>. Last accessed
636 28th October 2013.
- 637 [52] Lacombe VA, Hinchcliff KW, Taylor LE. Interactions of substrate availability, exercise
638 performance, and nutrition with muscle glycogen metabolism in horses. *J Am Vet Med*
639 *Assoc* 2003;223(11):1576-85.
- 640 [53] Snow DH, Harris RC. Effects of daily exercise on muscle glycogen in the Thoroughbred
641 racehorse. In: Persson SGB, Lindholm A, Jeffcott LB, editors. *Proceedings of the Third*
642 *International Conference on Equine Exercise Physiology*, Uppsala, Sweden, 15-19 July
643 1990, Davis, California: ICEEP Publications; 1991, p. 299-301.
- 644 [54] Hyppa S, Rasanen LA, Reeta Poso A. Resynthesis of glycogen in skeletal muscle from
645 Standardbred trotters after repeated bouts of exercise. *Am J Vet Res* 1997;58(2):162-6.

- 646 [55] Geor RJ. The role of nutritional supplements and feeding strategies in equine athletic
647 performance. *Equine Comp Exerc Physiol* 2006;3(3):109-19.
- 648 [56] Lacombe VA, Hinchcliff KW, Kohn CW, Devor ST, Taylor LE. Effects of feeding
649 meals with various soluble-carbohydrate content on muscle glycogen synthesis after exercise
650 in horses. *Am J Vet Res* 2004;65(7):916-23.
- 651 [57] Lindholm A, Bjerneld H, Saltin B. Glycogen depletion pattern in muscle fibres of
652 trotting horses. *Acta Physiol Scand* 1974;90:475-84.
- 653 [58] Harris RC, Marlin DJ, Snow DH. Metabolic response to maximal exercise of 800 and
654 2000m in the Thoroughbred horse. *J Appl Physiol* 1987;63(1):12-19. Available at:
655 <http://jap.physiology.org.ezproxy.is.ed.uk/content/63/1/12.full.pdf+html>. Last accessed 28th
656 October 2013.
- 657 [59] Hargreaves M. Interactions between muscle glycogen and blood glucose during
658 exercise. *Exercise Sport Sci R* 1997;25(1):21-40.
- 659 [60] Morifuji M, Kanda A, Koga J, Kawanaka K, Higuchi M. Preexercise ingestion of
660 carbohydrate plus whey protein hydrolysates attenuates skeletal muscle glycogen depletion
661 during exercise in rats. *J Nutr* 2011;27(7-8):833-7.
662
- 663 [61] Pagan JD, Essen-Gustavsson B, Lindholm A, Thornton J. The effect of dietary energy
664 source on exercise performance in Standardbred horses. In: Gillespie JR, Robinson NE,
665 editors. *Equine Exercise Physiology 2: Proceedings of the Second International Conference*
666 *on Equine Exercise Physiology, San Diego, California, 7-11 August, 1986*, Davis,
667 California: ICEEP Publications; 1987, p. 686-99.
- 668 [62] Cairns SP. Lactic acid and exercise performance: culprit or friend? *Sports Med*
669 2006;36(4):279-91.
- 670 [63] Bonen A. The expression of lactate transporters (MCT1 and MCT4) in heart and muscle.
671 *Eur J Appl Physiol* 2001;86(1):6-11. Available at:
672 <http://dx.doi.org/10.0007/s004210100516>. Last accessed 6th December 2013.

- 673 [64] Thomas C, Bishop D, Moore-Morris T, Mercier J. Effects of high-intensity training on
674 MCT1, MCT4, and NBC expressions in rat skeletal muscles: influence of chronic metabolic
675 alkalosis. *Am J Physiol-Endoc M* 2007;293:E916-E922. Available at:
676 <http://dx.doi.org/10.1152/ajpendo.00164.2007>. Last accessed 6th December 2013.
- 677 [65] Brooks GA. Cell-cell and intracellular lactate shuttles. *J Physiol*
678 2009;587(23):5591-600. Available at: <http://dx.doi.org/10.1113/jphysiol.2009.178350>. Last
679 accessed 9th December 2013.
- 680 [66] Kelso TB, Hodgson DR, Witt EH, Bayly WM, Grant BD, Gollnick PD. Bicarbonate
681 administration and muscle metabolism during high-intensity exercise. In: Gillespie JR,
682 Robinson NE, editors. *Proceedings of the Second International Conference on Equine*
683 *Exercise Physiology*, San Diego, California, August 7-11, 1986, Davis, California: ICEEP
684 Publications; 1987, p. 438-47.
- 685 [67] Lawrence LM, Miller PA, Bechtel PJ, Kane RA, Kurcz EV, Smith JS. The effect of
686 sodium bicarbonate ingestion on blood parameters in exercising horses. In: Gillespie JR,
687 Robinson NE, editors. *Proceedings of the Second International Conference on Equine*
688 *Exercise Physiology*, San Diego, California, August 7-11, 1986, Davis, California: ICEEP
689 Publications; 1987, p. 448-55.
- 690 [68] Mainwood GW, Worsley-Brown P. The effects of extracellular pH and buffer
691 concentration on the efflux of lactate from frog sartorius muscle. *J Physiol* 1975;250:1-22.
692 Available at:
693 <http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1348336/pdf/jphysiol00886-0023.pdf>. Last
694 accessed 9th December 2013.
- 695 [69] Connysson M, Muhonen S, Lindberg JE, Essen-Gustavsson B, Nyman G, Nostell K,
696 Jansson A. Effects on exercise response, fluid and acid-base balance of protein intake from
697 forage-only diets in Standardbred horses. *Equine Vet J* 2006;36:648-53.
- 698 [70] Glade MJ. Nutrition and performance of racing Thoroughbreds. *Equine Vet J*
699 1983;15(1):31-6.

- 700 [71] Miller-Graber PA, Lawrence LM, Foreman JH, Bump KD, Fisher MG, Kurcz EV.
701 Dietary protein level and energy metabolism during treadmill exercise in horses. J Nutr
702 1991;121:1462-9.
- 703 [72] Jansson A, Lindberg JE. Effects of forage-only diet on bodyweight and response to
704 interval training on a track. In: Saastamoinen MT, Martin-Rosset W, editors. Nutrition of the
705 Exercising Horse, Wageningen: Wageningen Academic Publishers; 2008, p. 345-9.
- 706 [73] Ellis AD, Hollands T, Allen DE. Effect of forage intake on bodyweight and
707 performance. Equine Vet J 2002;34:66-70.
- 708 [74] Kronfeld DS. Body fluids and exercise: Influences of nutrition and feeding
709 management. J Equine Vet Sci 2001;21(9):417-28.
- 710 [75] Meyer H. Influence of diet, exercise and water restriction on the gut fill in horses. Proc
711 Equine Nutr Physiol Soc 1995;14:90-1.
- 712 [76] Spooner HS, Nielsen BD, Schott II HC, O'Connor-Robinson CI, Harris PA. Hydration
713 status of horses performing endurance exercise: I. Evidence for a role of diet. Comp Exerc
714 Physiol 2013;9(3/4):189-97.
- 715 [77] Manuka Chaff, Quirindi, Australia
- 716 [78] Equi-Analytical Laboratories www.equi-analytical.com
- 717 [79] Fiber Fresh Feeds Ltd www.fiber-fresh.com

