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DAIRY COW GENOTYPE AND METABOLIC STATUS

12

13 **A comparison of energy balance and metabolic profiles of the New Zealand and**

14 **North American strains of Holstein Friesian dairy cow**

15

16 **J. Patton^{1,2}, J. J. Murphy¹, F. P. O'Mara², and S. T. Butler¹**

17 *¹Teagasc Moorepark, Dairy Production Research Centre, Fermoy, Co. Cork, Ireland*

18 *²School of Agriculture, Food Science and Veterinary Medicine, College of Life*

19 *Sciences, University College Dublin, Ireland*

20

21 Corresponding author: Stephen Butler. Email: stephen.butler@teagasc.ie

22 **Abstract**

23 The milk production, energy balance (EB), endocrine and metabolite profiles of 10
24 New Zealand Holstein-Friesian (NZ) cows and 10 North American Holstein-Friesian
25 (NA) cows were compared. The NA cows had greater peak milk yields and total
26 lactation milk yields (7387 vs. 6208 kg; s.e.d. = 359), lower milk fat and similar
27 protein concentrations compared to the NZ cows. Bodyweight was greater for NA
28 cows compared to NZ cows throughout lactation (596 vs. 544 kg; s.e.d. = 15.5), while
29 body condition score (BCS) tended to be lower. The NA strain tended to have greater
30 DMI (17.2 vs. 15.7 kg/d; s.e.d. = 0.78) for wk 1-20 of lactation, though DMI as a
31 proportion of metabolic bodyweight was similar for both strains. There were no
32 differences observed between the strains for the timing and magnitude of the energy
33 balance (EB) nadir, interval to neutral EB, or mean daily EB for week 1-20 of
34 lactation. Plasma concentrations of glucose and insulin were greater for NA cows
35 during the transition period (d 14 *pre partum* to d 28 *post partum*). Plasma IGF-I
36 concentrations were similar for the strains at this time, but NZ cows had greater
37 plasma IGF-I concentration from d 29 to d 100 of lactation, despite similar calculated
38 EB. In conclusion, the results of this study do not support the premise that the NZ
39 strain has a more favourable metabolic status during the transition period. The results
40 however indicate that NZ cows begin to partition nutrients towards body reserves
41 during mid-lactation whereas NA cows continue to partition nutrients to milk
42 production.

43

44 **Keywords:** Dairy cows, energy balance, nutrient partitioning, genetic selection

45 **Introduction**

46 Dairy cows typically enter a state of negative energy balance (NEB) *post*
47 *partum*, when the combined energy requirements for maintenance and milk
48 production exceed dietary energy intake. This energy deficit arises because cows
49 generally achieve peak milk production at an earlier stage than maximal feed intake
50 (Veerkamp, 1998). The shortfall in dietary intake is met by increased mobilization of
51 body reserves in support of lactation, which occurs through coordinated adaptation of
52 metabolism across several body tissues (Bauman, 2000).

53

54 The magnitude and duration of NEB is dependent on the direct and interactive
55 effects of numerous factors including genotype, plane of nutrition, and body
56 condition score (BCS) at calving. Consequently, there is considerable variation in the
57 degree of energy deficit experienced by individual cows, both within and between
58 studies. Genetic selection for increased milk yield has resulted in cows that are
59 predisposed to more severe NEB, as the correlated response in feed intake to selection
60 accounts for only approximately 45 to 65 percent of the increase in milk yield
61 (Veerkamp, 1998). A negative genetic correlation consequently exists between BCS
62 and genetic merit for milk yield (Berry et al., 2003).

63

64 There is compelling evidence of a negative genetic correlation between milk
65 production and fertility performance (Hansen, 2000). Though the precise mechanisms
66 remain unresolved, increasing negative energy balance (NEB) and altered partitioning
67 of dietary energy have been cited as being detrimental to reproductive efficiency
68 (Butler, 2003). This is further intimated by negative genetic correlations identified
69 between body condition score (BCS) and fertility performance (Pryce et al., 2001).

70 Strain comparison studies in New Zealand and Ireland have reported lower milk
71 volume, higher BCS throughout lactation and superior reproductive performance for
72 the New Zealand (NZ) Holstein Friesian compared to North American (NA) Holstein
73 Friesian (Harris and Kolver, 2001; Horan et al., 2005b). The NA strain has been
74 selected for increased milk yield, body size and angularity in a production system
75 based on year-round calving and high levels of concentrate supplementation, with
76 little emphasis traits such as fertility. The NZ strain has been selected for increased
77 milk solids yield and improved fertility and survival in a pasture-based production
78 system (Horan et al., 2005a). The strain comparison model provides a framework for
79 examining the effects of divergent genetic selection programmes within the Holstein
80 Friesian on energy balance and nutrient partitioning. The objective of the current
81 study was therefore to characterize the energy balance, nutrient partitioning and
82 metabolic profiles of the NA and NZ strains, which differ in genetic merit for milk
83 production.

84

85 **Materials and Methods**

86 *Animals and experimental design*

87 Two groups of 10 spring-calving, multiparous Holstein-Friesian cows were
88 selected from the NA and NZ groups of the Moorepark strain comparison study
89 (Horan et al., 2005a). The origins and establishment of the experimental groups from
90 which the cows were selected have been previously described by Horan et al. (2005a).
91 The North American (NA) strain was developed by mating the top 50% of cows in
92 Moorepark (based on pedigree index for milk production) with 5 NA Holstein-
93 Friesian sires, selected as the highest available in Ireland for pedigree index for milk
94 production. The NZ strain were imported as embryos from New Zealand and

95 implanted into Holstein heifers. These embryos were generated by mating high
96 genetic merit NZ Holstein-Friesian cows with 5 high genetic merit NZ Holstein-
97 Friesian sires (based on Breeding Worth; the New Zealand genetic evaluation
98 system). The experimental animals used in the current study were selected from the
99 existing NA and NZ treatment groups involved in the Moorepark strain comparison
100 study (Table 1). Mean calving dates were 25th February (s.d. 18 days) for the NA
101 group and 2nd March (s.d. 17 days) for the NZ group.

102

103 ***Insert Table 1 Here***

104 The cows were housed in a free-stall barn from 3 weeks prior to the expected
105 calving date, with the treatment groups sharing common accommodation space. The
106 cows were trained to use the Griffith Elder feeding system (Griffith Elder Ltd, Bury
107 St Edmunds, Suffolk, UK). Forage and concentrate allocations were fed separately.
108 Forage mangers were mounted on electronic load cells, while concentrates were
109 dispensed through automatic feeders. Cows had *ad libitum* access to forage, which
110 was offered to allow for feed refusals of at least 5%. Refusals were removed daily.
111 The *pre partum* diet comprised *ad libitum* grass silage, with 2 kg per day of the
112 lactating concentrate (Table 2) introduced from 2 weeks prior to the expected calving
113 date. The *post partum* diet consisted of *ad libitum* grass silage and 8 kg of
114 concentrate. From March 20th, all lactating cows were offered zero-grazed grass (*L.*
115 *perenne spp*) supplemented with 4kg concentrate. Grass was harvested and fed each
116 morning. The chemical composition of the grass silage and zero-grazed grass is
117 reported in Table 3. Cows were turned out to pasture on July 30th and were offered
118 high quality grazed grass (*L. perenne spp.*) plus 4 kg/day of concentrate. Cows
119 remained at pasture day and night until mid-November, after which they were housed

120 at night. After December 1st, the cows were housed day and night. Animals were fed
121 grass silage *ad libitum* when housed.

122

123 ***Insert Table 2 here***

124 ***Insert Table 3 here***

125

126 *Samples and animal measurements*

127 Milk yield (kg) was recorded daily at the morning and evening milkings using
128 electronic milk meters (Dairy Master, Causeway, Co. Kerry, Ireland). Milk
129 composition (fat, protein and lactose) was determined on two days per week from
130 successive morning and evening milk samples by automated infra-red absorption
131 analysis using a Milkoscan 605 (Foss Electric, Hillerod, Denmark). Solids-corrected
132 milk (SCM) yield was calculated using the equation of Tyrell and Reid (1965). All
133 cows were dried off on December 15th, resulting in mean lactation length of 290 days
134 (s.d. 14 days) for the NA strain and 287 days (s.d. 16 days) for the NZ strain.

135 Samples of grass silage and concentrates offered were collected twice weekly
136 for chemical analysis. Zero-grazed grass was sampled daily for dry matter; samples
137 were bulked by week for composition analysis.

138 Cow body weight (kg) and BCS (Lowman et al., 1976) were recorded once
139 weekly from 3 weeks before the expected calving date, immediately post-calving, and
140 once weekly thereafter until the end of lactation. The dry cows were weighed before
141 feeding in the morning and the lactating cows were weighed after morning milking,
142 before feeding. Data were lost for pre-calving bodyweights and BCS owing to a
143 technical failure in the recording system. Energy balance, bodyweight, and BCS
144 profiles are therefore reported commencing from the week of calving

145 Blood samples were collected three times weekly (Monday, Wednesday,
146 Friday) by coccygeal venipuncture for 2 weeks before expected calving date, daily
147 from day of calving until day 14 *post partum*, and twice weekly (Monday, Thursday)
148 from day 15 to day 100 *post partum*. Sampling took place after the morning milking
149 and before feeding. Samples were collected into vials containing lithium heparin as an
150 anticoagulant. The samples were immediately centrifuged at $2000 \times g$ for 10 minutes.
151 The plasma was decanted and stored at -20°C until analysis.

152 *Laboratory procedures and analysis*

153 The DM, NDF, crude fiber and CP of the forage and concentrate samples were
154 analyzed as described by McNamara et al. (2003). Determination of *in vitro* dry
155 matter digestibility (DMD) was carried out by near-infrared spectroscopy using a
156 NIRsystems 6500 spectrophotometer (Perstorp Analytical Incorporated, Silver
157 Springs, Maryland, USA). Silage pH was measured on the juice pressed from the
158 silage using a glass electrode and a pH meter (Radiometer pHM2 standard pH meter-
159 radiometer, Copenhagen). The organic matter digestibility of grass was determined as
160 described by Morgan et al. (1994)

161 Blood plasma was analysed for glucose, non-esterified fatty acid (NEFA), and
162 beta-hydroxybutyrate (BHBA) concentrations by enzymatic colorimetry, using
163 appropriate kits and an ABX Mira autoanalyzer (ABX Mira, Cedex 4, France).
164 Plasma insulin concentration was determined using a solid-phase fluoroimmunoassay
165 (AutoDELFIA, PerkinElmer Life and Analytical Sciences, Turku, Finland). The inter-
166 and intra-assay coefficients of variation were 14.7% and 6.4%, respectively.
167 Circulating IGF-1 concentrations were quantified using a validated double-antibody
168 radioimmunoassay, following ethanol:acetone:acetic acid (60:30:10) extraction as
169 described by Enright et al. (1989). Recombinant human IGF-1 (supplied by R&D

170 Systems Europe, UK) was used for iodination and standards (iodine – 125 supplied by
171 PerkinElmer (Unitech BD Ltd., Dublin, Ireland), as described by Spicer et al (1990).
172 The rabbit anti-human IGF-I (AFP4892898) was obtained through the US National
173 Hormone and Peptide Program (Dr A F Parlow, Scientific Director). Inter- and intra-
174 assay coefficients of variation were 17.0 and 11.6%.

175

176 *Energy balance*

177 Energy balance was estimated as the difference between energy intake and the
178 sum of energy for maintenance and milk production. The French Net Energy (NE)
179 system was used (Jarrige, 1989). The NE content of the concentrates offered was
180 determined using the NE values (UFL) of ingredients (INRAtion, 1999, version 2.7).
181 One UFL is the NE content of 1 kg of air-dry standard barley for milk production
182 (Jarrige, 1989). The NE value of the grass silage was calculated based on its *in vitro*
183 DMD concentration (O'Mara et al., 1997). The NE value of the grass was determined
184 according to Jarrige (1989).

185 The following equations were used to determine the energy required for
186 maintenance and the energy output in milk:

187 Energy requirement for maintenance: $(\text{UFL}/\text{day}) = 1.4 + 0.6 \text{ BW}/100$

188 UFL requirement for milk: $(\text{UFL}/\text{kg of milk}) = 0.0054\text{FC} + 0.0031\text{PC} + 0.0028\text{LC} -$
189 0.015 ; where BW = body weight, FC = fat concentration, PC = protein concentration
190 and LC = lactose concentration all in g/kg.

191

192 *Data handling and statistical analysis*

193 Daily milk yield and DMI data were collapsed into weekly means, and EB
194 values were similarly calculated as weekly means. Repeated measures analyses of
195 genotype effects on DMI, milk yield, milk composition, plasma metabolites, insulin
196 and IGF-I, energy balance, BCS and bodyweight were carried out using the MIXED
197 procedure of SAS (SAS Institute, 1991). A first order autoregressive covariance
198 structure was used. Genotype, time, and the interaction of genotype and time were
199 included as fixed effects. Cow within genotype was included as a random effect. For
200 illustrative purposes (Figure 4), body weight and BCS lines were smoothed using the
201 LOESS procedure in SAS (SAS Institute, 1991).

202 Data for plasma analytes during daily blood sampling from day 1 to day 14
203 *post partum* were collapsed into four mean values (day 1 to 3 = day 3; day 4 to 7 =
204 day 7; day 8 to 10 = day 10; day 11 to 14 = day 14), and into weekly mean values for
205 *pre partum* samples and *post partum* samples collected from day 14 to 100 post-
206 calving. This resulted in all cows having plasma analyte data for days -14, -7, 0, 3, 7,
207 10, 14, 21, 28, 35, 42, 49, 56, 63, 70, 84, 91, and 98 for statistical analysis. Plasma
208 insulin, IGF-I and metabolite data were not normally distributed, and were log
209 transformed prior to statistical analysis. Plasma analyte data for each cow was divided
210 into 2 time periods (transition period from d 14 *pre partum* to d 28 *post partum*; post-
211 transition period from d 29 to d 100 *post partum*) and the time periods were analyzed
212 separately to accommodate the constant variance assumption of repeated measures
213 analysis. Results for plasma analytes were back-transformed and are presented as
214 geometric means (and 95% confidence intervals).

215

216 **Results**

217 *Milk production and composition*

218 The NA strain had a greater milk yield ($P < 0.01$) during week 1-20 of
219 lactation, and tended to have a greater SCM yield ($P = 0.06$) compared to the NZ
220 strain (Table 4). The NA strain had a higher ($P < 0.001$) peak milk yield, but peak
221 SCM yield did not differ between the strains ($P = 0.39$). Mean daily SCM yield from
222 wk 20 until the end of lactation was 18.8 kg and 15.1 kg ($P < 0.01$, s.e.d. 1.4 kg) for
223 the NA and NZ strains, respectively.

224

225 *Insert Table 4 here*

226

227 Milk fat concentration over the full lactation was greater for NZ cows ($P < 0.01$),
228 while milk protein concentration did not differ between the strains ($P = 0.33$). Total
229 combined yield of milk fat and protein over the full lactation was 12.7% greater ($P =$
230 0.03) for the NA strain (Table 4). The NA strain produced 20.4% greater volume ($P <$
231 0.01) of milk over the full lactation compared to the NZ strain; total lactation SCM
232 yield was 12.7% greater ($P = 0.04$) for the NA strain (Figure 1).

233

234 *Insert Figure 1 here*

235

236 *Dry matter intake, energy balance and feed efficiency*

237 Mean DMI ($P = 0.07$) and net energy intake ($P = 0.08$) tended to be greater for
238 NA compared to NZ cows (Figure 2) during wk 1-20 of lactation. When expressed as
239 a percentage of metabolic bodyweight, however, the strains had similar ($P = 0.78$)
240 mean daily DMI over the same time period (Table 5).

241

242 *Insert Table 5 here*

243 *Insert Figure 2 here*

244

245 The NA and NZ strains had similar mean daily calculated energy balance
246 (EB) during week 1-20 ($P = 0.95$) of lactation (Figure 3). The strains also had a
247 similar magnitude of EB nadir ($P = 0.72$). In addition, the timing of EB nadir ($P =$
248 0.77) and interval to neutral EB ($P = 0.87$) did not differ between the two strains
249 (Table 5).

250

251 *Insert Figure 3 here*

252

253 The NA and NZ strains had similar milk yield per kg of DMI ($P = 0.22$), and
254 similar output of milk energy per unit of net energy intake ($P = 0.91$), for week 1-20
255 of lactation (Table 5). Solids corrected milk yield as a proportion of metabolic
256 bodyweight did not differ between the strains ($P = 0.57$).

257

258 *Bodyweight and body condition score*

259 The NA and NZ strains had similar BCS at the beginning of lactation (3.17 vs.
260 3.22, respectively; s.e.d = 0.18; $P = 0.78$). The strains had lost a similar amount of
261 BCS by week 20 of lactation (0.65 vs. 0.55 respectively; s.e.d = 0.15; $P = 0.53$).
262 Thereafter, the NZ strain began to increase in BCS whereas the NA strain did not,
263 resulting in a greater BCS for NZ compared to NA by the end of lactation (2.85 vs.
264 2.43 respectively; s.e.d = 0.15; $P = 0.02$) Mean bodyweight across the full lactation
265 was greater for NA compared to NZ cows (596 vs. 544 kg respectively; s.e.d = 21.9;
266 $P = 0.02$) (Figure 4).

267

268 *Insert Figure 4 here*

269

270 *Plasma insulin, IGF-I and metabolites*

271 Mean plasma insulin concentration was higher ($P = 0.01$) for the NA strain
272 during the transition period, and tended to be higher ($P = 0.06$) from d 29 until d 100
273 (Figure 5; Table 6). There were no differences between the strains in mean plasma
274 concentrations of IGF-I in the transition period ($P = 0.71$). However, the NZ strain
275 had higher ($P = 0.04$) plasma IGF-I concentrations from d 29 to d 100 of lactation
276 (Figure 5; Table 6).

277

278 *Insert Figure 5 here*

279 *Insert Table 6 here*

280

281 Plasma glucose concentration was higher for the NA strain during the
282 transition period ($P = 0.01$), but differences were not observed in the post-transition
283 period (d 29 to d 100 of lactation) ($P = 0.21$) (Figure 6; Table 6). There were no
284 differences observed between the strains in mean plasma NEFA concentration, either
285 during the transition period ($P = 0.29$), or during the post-transition period ($P = 0.99$).
286 Plasma BHBA concentration was higher for NZ compared to NA cows during the
287 transition period ($P = 0.02$), but both strains had similar mean plasma BHBA
288 concentrations during the post-transition period ($P > 0.05$).

289

290 **Discussion**

291 The primary objective of this study was to characterize the EB, nutrient
292 partitioning and metabolic profiles of the NA and NZ strains, which differ in their

293 genetic merit for milk production, BCS and fertility performance (Horan et al.,
294 2005b). The lack of difference between the EB profiles of the strains during early
295 lactation was particularly interesting given the extensive reports of negative genetic
296 relationships between milk yield and both EB and BCS (Berry et al., 2003; Veerkamp
297 and Thompson, 1999).

298

299 In general, cows of higher genetic merit for milk yield have greater milk
300 energy output in early lactation, which is met by a combination of increased DMI and
301 body tissue mobilization (Bauman, 2000). The higher milk yield recorded for the NA
302 cows in the present study is a result of more intensive genetic selection for milk yield
303 compared to NZ cows (Kolver et al., 2000). Peak daily milk yield was higher for the
304 NA strain as had been reported previously (Horan et al., 2005a), however peak yield
305 did not differ between the groups when expressed as SCM. This was primarily due to
306 the higher milk fat concentration of the NZ strain; mean milk protein concentration
307 was not different between the groups. The NZ strain has previously exhibited higher
308 milk fat and milk protein in pasture-based production systems (Horan et al., 2005a).
309 Increasing fat and protein yield in a given volume of milk has been a key breeding
310 objective in the New Zealand breeding programme for many years (Harris and
311 Kolver, 2001). It can be therefore concluded that the strains experienced a
312 comparable magnitude of milk energy demand at peak SCM production.

313

314 The NA strain had approximately 1.5 kg per day greater DMI, equivalent to
315 1.26 UFL of NE intake per day, compared to the NZ strain from wk 1-20 *post*
316 *partum*. However, the daily energy requirements for milk and maintenance during
317 this time were approximately 1.0 UFL and 0.30 UFL greater for the NA strain

318 respectively, resulting in similar EB profiles for the strains. The higher DMI of the
319 NA cows may be attributable to their greater bodyweight, as bodyweight is highly
320 correlated with DMI (Veerkamp and Thompson, 1999). The difference in bodyweight
321 between the strains is a direct result of divergent genetic selection objectives within
322 the strains' respective breeding programmes. The NA strain has been selected for
323 increased body size (Hansen, 2000), whereas bodyweight is afforded a negative
324 economic weighting in NZ selection indices (Harris et al, 1996).

325

326 Consistent with the EB results, the BCS profiles of the strains were not
327 different for weeks 1-20 of lactation. The profiles subsequently diverged however, as
328 the NZ cows began to increase BCS while the NA cows failed to gain BCS,
329 indicating that the NZ cows were in a more positive nutritional status during mid to
330 late lactation. Similarly McCarthy et al. (2007a) reported no difference in the rate of
331 BCS change between NA and NZ cows during early lactation, but a greater rate of
332 BCS accretion post nadir for NZ cows.

333

334 Differences in milk yield between high and low genetic merit cows are less on
335 a high grass diet because intake is limited by constraining factors in the diet such as
336 physical bulk, whereas on high concentrate diets, high genetic merit cows have the
337 advantage of higher DM intakes (Kennedy et al., 2003). The NA strain achieves a
338 lower proportion of potential DMI and milk yield in a pasture system compared to the
339 NZ strain, which is evidenced by its greater milk yield response to concentrate
340 supplementation (Horan et al., 2005a). Similarly, McCarthy et al (2007b) reported a
341 lower substitution rate of pasture for concentrate by the NA strain compared to the
342 NZ strain. This explains the greater milk yield response of NA cows to concentrate

343 supplementation, and demonstrates that the greater lactation energy demands of the
344 NA strain are not satisfied by a predominantly pasture diet. Furthermore, the same
345 study noted that despite their lower milk production, NZ cows spend a greater
346 proportion of time grazing than NA cows and tend to increase grazing time when feed
347 allowance is reduced, suggesting that the NZ strain may be more adapted to a grazing
348 scenario (McCarthy et al., 2007b). The BCS profiles observed in the current study
349 and similar strain comparisons (McCarthy et al., 2007a; Roche et al., 2006) indicate
350 that the inability of the NA strain to meet energy demands from pasture persists
351 through lactation. In contrast, the NZ strain is capable of ingesting sufficient energy
352 for milk production and body tissue accretion from mid-lactation in a pasture-based
353 system.

354

355 The SCM yield of the NA cows was greater than NZ cows from
356 approximately wk 20 until the end of lactation, coincident with the divergence of the
357 BCS profiles of the strains. Similarly, Horan et al. (2006) observed that NA cows had
358 a greater milk yield response to additional concentrate supplementation than NZ
359 cows. Energy partitioning results in the current study were not confounded by
360 pregnancy status as breeding was delayed due to a concurrent embryo collection
361 study which prevented cows from becoming pregnant during the duration of the
362 study. The divergence in the milk production and BCS profiles of the strains therefore
363 indicates that the NA cows maintain preferential partitioning of nutrients to the
364 mammary gland for a longer duration than NZ cows.

365

366 While it is well established that nutrient partitioning changes with stage of
367 lactation (Kirkland and Gordon, 2001), the temporal change in the magnitude of

368 differences between the strains is an interesting feature of the present study. Genetic
369 selection for increased milk yield has been associated with the shifting of
370 homeorhetic controls, such that milk production is maximised from ingested nutrients
371 and available body tissue reserves, particularly during early lactation (Bauman, 2000).
372 However, the NA and NZ strains had a comparable degree of NEB and a similar
373 propensity for body tissue mobilization during early lactation; differences in nutrient
374 partitioning did not become manifest until after the time of peak milk energy demand.
375 This implies that strain differences exist in the timescale of homeorhetic adaptations
376 during lactation, with the NZ strain affording a greater metabolic priority to
377 replenishment of body reserves at an earlier stage of lactation than the NA strain.

378

379 The NA cows had increased plasma insulin concentrations during the
380 transition period, despite the similar calculated EB of the strains at this time.
381 Differences in plasma insulin concentration, though statistically significant, were
382 modest. In contrast, others have reported lower plasma insulin concentration for cows
383 of higher genetic merit for milk yield (Gutierrez et al., 2006). The increased plasma
384 glucose concentration for the NA cows was consistent with the observed differences
385 in insulin concentrations.

386

387 The temporal patterns of plasma IGF-I concentration observed were similar to
388 previous reports, with a decline at parturition and a gradual increase thereafter
389 (McGuire et al., 1995). While the strains had similar plasma IGF-I profiles during the
390 transition period, plasma IGF-I was higher for NZ cows from approximately d 30 of
391 lactation. This occurred despite the similar EB profiles between the strains, and the
392 higher plasma insulin concentrations in the NA cows.

393

394 Expression of the IGF-I gene in the liver is acutely responsive to nutritional
395 status. The decline in IGF-I concentration at parturition is due to reduced expression
396 of growth hormone receptor 1A (GHR-1A) and IGF-I mRNAs, coincident with a
397 period of liver refractoriness to growth hormone (Radcliff et al., 2003). A several-fold
398 increase in insulin has been shown to stimulate hepatic expression of GHR-1A and
399 IGF-I mRNA (Butler et al., 2003; Rhoads et al., 2004). The higher insulin
400 concentration for NA cows during the transition period in the current study may have
401 been insufficient to elicit a detectable increase in plasma IGF-I concentration. Indeed,
402 Radcliff et al (2006) showed that restricting DMI in early lactation decreased the rate
403 of *post partum* increase in liver GHR mRNA and tended to reduce plasma IGF-I
404 concentration, but had no effect on liver IGF-I mRNA. This indicates that post-
405 transcriptional and/or post-translational mechanisms may also exert control on *post*
406 *partum* IGF-I concentrations. Plasma IGF-I was higher for NZ cows from
407 approximately day 30-100 of lactation, despite the similar EB profiles and lower
408 circulating insulin concentrations compared to NA cows. Crooker et al. (2001)
409 likewise showed that although *post partum* EB did not differ between cows of high
410 and low genetic merit, plasma IGF-I was lower for the high genetic merit cows.
411 Genetic selection for milk yield may therefore affect the somatotropic axis during
412 early lactation independent of energy balance.

413

414 Gross energy efficiency may be defined as energy in the milk produced
415 divided by the total energy intake (Brody, 1945). Gross efficiency is greater if
416 calculated when cows are mobilizing body tissue in support of milk production,
417 because the potential contribution of body reserves to milk energy output is not

418 considered (Veerkamp and Emmans, 1995). The strains had a similar degree of BCS
419 change over the first 20 weeks of lactation in the present study; the results thus
420 demonstrate that the NA and NZ strains have a similar level of milk production per
421 unit of energy intake or bodyweight, net of differences in body fat mobilization. This
422 is consistent with the review of Bauman et al. (1985), who stated that there is little
423 genetic variation in the partial efficiencies of metabolizable energy utilization for
424 maintenance or milk production. There is however a considerable degree of genetic
425 variation in gross efficiency, principally due to a dilution of maintenance
426 requirements for higher yielding cows (Veerkamp and Emmans, 1995). Similarly,
427 Yerex et al. (1988) showed that cows selected for lower bodyweight had lower
428 maintenance requirements, and consequently a higher gross efficiency than heavier
429 cows with similar levels of milk yield. In the present study, the lower milk
430 production of the NZ cows was offset by lower DMI and bodyweight to result in
431 similar milk production efficiencies for the strains.

432

433 **Conclusions**

434

435 This study compared the EB, metabolic profiles and nutrient partitioning of the NA
436 and NZ strains of Holstein Friesian. The NZ strain had similar SCM yield, lower
437 maintenance requirements and lower DMI in early lactation compared to the NA
438 strain, resulting in no difference in EB between the strains. The similarity in early
439 lactation EB of the strains was reflected in their respective metabolic and endocrine
440 profiles during that time. The NZ cows began to replenish BCS at an earlier stage of
441 lactation, and had greater plasma concentrations of IGF-I from approximately wk 4 of
442 lactation. In conclusion, the results of this study do not support the premise that the
443 NA cows experience a greater dietary energy deficit during the transition period due
444 to their superior genetic potential for milk yield. The results do however indicate that
445 NZ cows begin to partition nutrients towards body reserves during mid-lactation
446 whereas NA cows continue to preferentially partition nutrients to milk for a longer
447 duration *post partum*

448

449

450

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452

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622 **Table 1** Genetic merit of the North American and New Zealand strains of Holstein

623 Friesian based on predicted differences² and standard deviations (SD) for milk

624 production, calving interval and survival

| Trait | Strain ¹ | |
|-------------------------|---------------------|---------------|
| | NA | NZ |
| Milk (kg) | + 210 (117) | + 1 (157) |
| Fat (kg) | + 6.2 (3.5) | + 6.5 (5.0) |
| Protein (kg) | + 7.4 (4.4) | + 3.7 (4.0) |
| Fat (g/kg) | + 0.10 (1.4) | + 1.13 (0.62) |
| Protein (g/kg) | + 0.40 (0.32) | + 0.75 (0.43) |
| Calving interval (days) | + 0.99 (1.98) | - 2.86 (1.53) |
| Survival (%) | + 0.04 (0.29) | + 1.14 (0.48) |

625 ¹NA = North American Holstein Friesian; NZ = New Zealand Holstein Friesian

626 ²All predicted differences obtained from the February 2004 international evaluations of the
627 INTERBULL Animal Centre (Uppsala, Sweden).

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634 **Table 2** *Ingredient and chemical composition of concentrate supplement fed*
 635 *throughout the study*

| Ingredient | Value |
|--|-----------------------|
| Barley (g/kg) | 200 |
| Beet pulp (g/kg) | 220 |
| Maize gluten (g/kg) | 170 |
| Rapeseed meal (g/kg) | 210 |
| Soybean meal (g/kg) | 140 |
| Lard (g/kg) | 30 |
| Di-calcium phosphate (g/kg) | 15 |
| Limestone flour (g/kg) | 7 |
| Salt (g/kg) | 5 |
| Calcined magnesite (g/kg) | 3 |
| <i>Chemical Composition</i> | |
| Dry matter (g/kg) | 871 ¹ ± 32 |
| Crude protein (g/kg DM) | 186 ± 71 |
| Neutral detergent fibre (g/kg DM) | 256 ± 20 |
| Ash (g/kg DM) | 91 ± 3 |
| Starch (g/kg DM) | 182 ± 15 |
| Net energy (UFL/kg) ² | 1.0 |
| NE _L (Mcal/kg) ³ | 1.7 |

636 ¹Mean ± standard deviation

637 ² Estimated based on net energy values for ingredients (INRAtion, 1999, version 2.7).

638 ³ Estimated based on 1 UFL = 1.7 Mcal/kg (Vermorel, 1989)

639 **Table 3** *Chemical composition of grass silage and zero-grazed grass*¹

| Variable | Grass silage | Zero-grazed grass |
|--|--------------|-------------------|
| Dry matter (DM), (g/kg) | 273 ± 53 | 172 ± 22 |
| Crude protein (g/kg DM) | 117 ± 9 | 155 ± 31 |
| Neutral detergent fibre (g/kg DM) | 589 ± 27 | 390 ± 23 |
| Acid detergent fibre (g/kg DM) | 368 ± 23 | - |
| Ash (g/kg DM) | 58.3 ± 8 | 78.7 ± 8 |
| Dry matter digestibility ² (g/kg) | 697 ± 40 | - |
| Organic matter digestibility (g/kg DM) | 630 ± 33 | 813 ± 17 |
| pH | 4.11 ± 0.36 | - |
| Net energy ^{3,4} (UFL/kg DM) | 0.79 | 0.99 |
| Net energy ⁵ (Mcal/kg DM) | 1.34 | 1.68 |

640 ¹ Values reported are means ± standard deviation

641 ² Estimated using near-infrared spectroscopy

642 ³ The net energy value of silage was calculated from its *in vitro* DMD concentration (O'Mara *et al.*,
643 1997)

644 ⁴ The net energy value of grass was determined according to Jarrige (1989)

645 ⁵ Estimated based on 1 UFL = 1.7 Mcal/kg (Vermorel, 1989)

646

647 **Table 4** *Effect of strain¹ of Holstein Friesian on milk production and composition*

| Variable | NA | NZ | s.e.d. ² | P-value |
|---|------|------|---------------------|---------|
| <i>Week 1-20 of Lactation</i> | | | | |
| Milk yield (kg/day) | 30.9 | 26.8 | 1.1 | <0.01 |
| Solids corrected milk ³ (SCM) yield (kg/day) | 29.6 | 27.7 | 1.0 | 0.06 |
| Milk fat content (g/kg) | 42.0 | 47.7 | 1.8 | <0.01 |
| Milk protein content (g/kg) | 32.4 | 32.5 | 0.6 | 0.97 |
| Peak Milk yield (kg) | 37.6 | 32.7 | 1.1 | <0.001 |
| Peak SCM yield (kg) | 38.0 | 36.6 | 1.6 | 0.39 |
| <i>Total Lactation⁴</i> | | | | |
| Milk yield (kg) | 7280 | 6045 | 362 | <0.01 |
| SCM (kg) | 6816 | 6048 | 342 | 0.04 |
| Milk fat content (g/kg) | 40.2 | 43.9 | 1.2 | <0.01 |
| Milk protein content (g/kg) | 33.5 | 34.1 | 0.6 | 0.33 |
| Total fat + protein yield (kg) | 533 | 473 | 27 | 0.03 |

648 ¹ NA= North American Holstein Friesian; NZ= New Zealand Holstein Friesian

649 ² SED = Standard error of difference

650 ³ Calculated as described by Tyrell and Reid (1965)

651 ⁴ Mean lactation length was 287d for NZ and 290d for NA strain

652 **Table 5** *Effect of strain on Energy Balance and Feed Intake*

| Variable | NA ¹ | NZ ¹ | s.e.d. ² | P-Value |
|--|-----------------|-----------------|---------------------|---------|
| <i>Dry Matter and Energy Intake wk1-20</i> | | | | |
| Dry matter intake (DMI) (kg / d) | 17.2 | 15.7 | 0.78 | 0.07 |
| Net energy intake (UFL /d) | 16.8 | 15.5 | 0.70 | 0.08 |
| DMI as proportion of MBW ³ (%) | 14.3 | 14.1 | 0.71 | 0.78 |
| <i>Energy Balance (EB)</i> | | | | |
| EB wk 1-20 (UFL ⁴ / d) | -1.80 | -1.84 | 0.66 | 0.95 |
| Nadir EB (UFL / d) | -6.88 | -7.31 | 1.20 | 0.72 |
| Interval to nadir EB (days) | 10.3 | 10.6 | 1.84 | 0.77 |
| Interval to neutral EB (days) | 72 | 73 | 9.5 | 0.87 |
| <i>Milk Production Efficiency wk1-20</i> | | | | |
| Milk yield per kg DMI (kg) | 1.86 | 1.75 | 0.08 | 0.22 |
| UFL milk per UFL intake (UFL) | 0.84 | 0.85 | 0.12 | 0.91 |
| SCM ⁵ as proportion of MBW (%) | 17.7 | 18.1 | 0.71 | 0.57 |

653 ¹NA= North American Holstein Friesian; NZ= New Zealand Holstein Friesian654 ² s.e.d. = Standard error of difference655 ³MBW = Metabolic bodyweight, calculated as $B^{0.75}$, where B=bodyweight (kg)656 ⁴1 UFL = Net energy for lactation equivalent of 1 kg standard air-dry barley (Jarrige, 1989)657 ⁵SCM = Solids Corrected Milk

658 **Table 6** *Effect of strain on plasma concentrations¹ of insulin, IGF-I and metabolites*

| Variable | NA ² | NZ ² | Mean ratio ³ | P-value |
|--------------------------------------|-------------------|--------------------|-------------------------|---------|
| <i>Transition Period⁴</i> | | | | |
| Insulin (uIU/mL) | 4.39 (3.82, 5.16) | 3.32 (2.86, 3.82) | 1.33 (1.08, 1.65) | 0.01 |
| IGF-I (ng/mL) | 56.8 (49.4, 66.7) | 59.2 (51.4, 68.7) | 0.96 (0.78, 1.19) | 0.71 |
| Glucose (Mmol/L) | 3.50 (3.39, 3.63) | 3.29 (3.16, 3.39) | 1.07 (1.01, 1.12) | 0.01 |
| NEFA (Mmol/L) | 0.34 (0.28, 0.41) | 0.39 (0.33, 0.47) | 0.85 (0.66, 1.11) | 0.29 |
| BHB (Mmol/L) | 0.63 (0.57, 0.70) | 0.77 (0.69, 0.87) | 0.82 (0.70, 0.96) | 0.02 |
| <i>Post Transition⁴</i> | | | | |
| Insulin (uIU/mL) | 4.66 (4.06, 5.42) | 3.86 (3.35, 4.44) | 1.21 (0.99, 1.48) | 0.06 |
| IGF-I (ng/mL) | 77.5 (67.4, 90.0) | 97.5 (83.9, 112.2) | 0.80 (0.65, 0.99) | 0.04 |
| Glucose (Mmol/L) | 3.25 (3.19, 3.35) | 3.32 (3.25, 3.42) | 0.98 (0.95, 1.01) | 0.21 |
| NEFA (Mmol/L) | 0.17 (0.14, 0.20) | 0.17 (0.14, 0.20) | 1.00 (0.78, 1.29) | 0.99 |
| BHB (Mmol/L) | 0.46 (0.41, 0.51) | 0.44 (0.39, 0.48) | 1.05 (0.92, 1.21) | 0.45 |

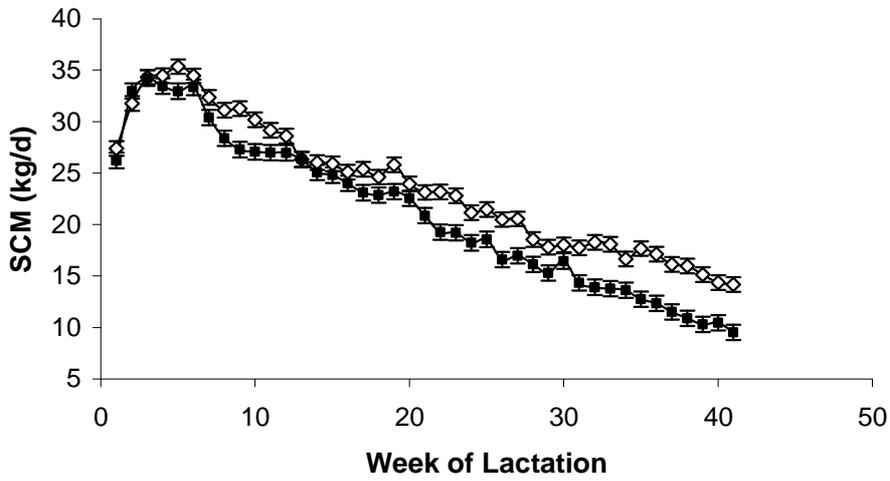
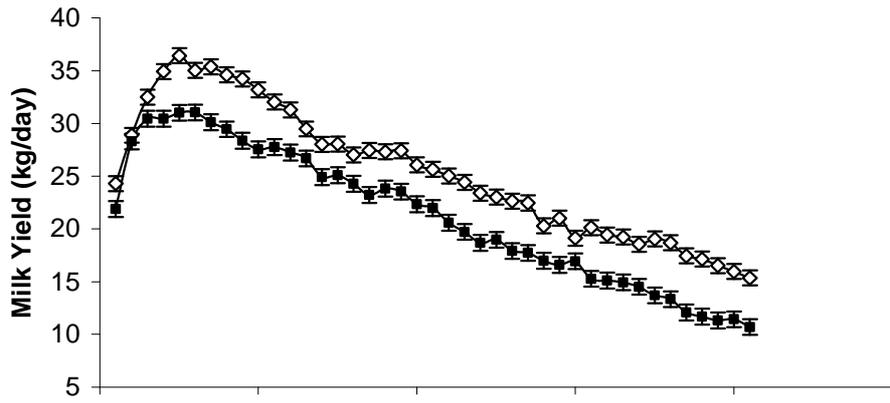
659 ¹Geometric Means (95% Confidence interval in parentheses)

660 ²NA = North American Holstein Friesian; NZ = New Zealand Holstein Friesian

661 ³Ratio of geometric means (95% Confidence interval in parentheses)

662 ⁴Transition = d 15 *pre partum* to d 28 *post partum*; Post transition = d 29 to 100 *post partum*

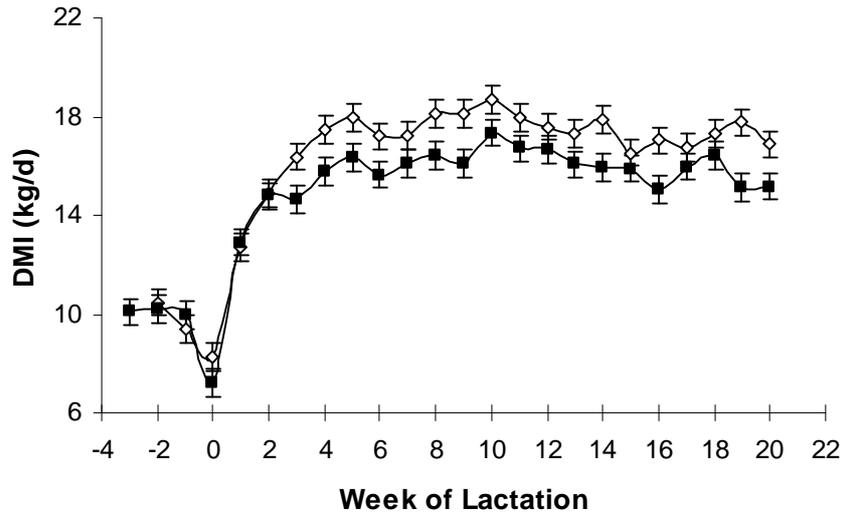
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Figure 1.

674 **Figure 1.** Effect of strain of Holstein-Friesian on milk yield and solids-corrected milk yield (SCM) (◇
675 = North American Holstein Friesian; ■ = New Zealand Holstein Friesian). The P values for the effects
676 of strain, week and interaction between strain and week on mean daily milk yield were 0.002, <0.001
677 and 0.96, respectively. The s.e.d. was 1.18 kg/day. The P values for the effects of strain, week and
678 interaction between strain and week on mean daily SCM yield were 0.04, <0.0001 and 0.98,
679 respectively. The s.e.d. was 1.05 kg/day.
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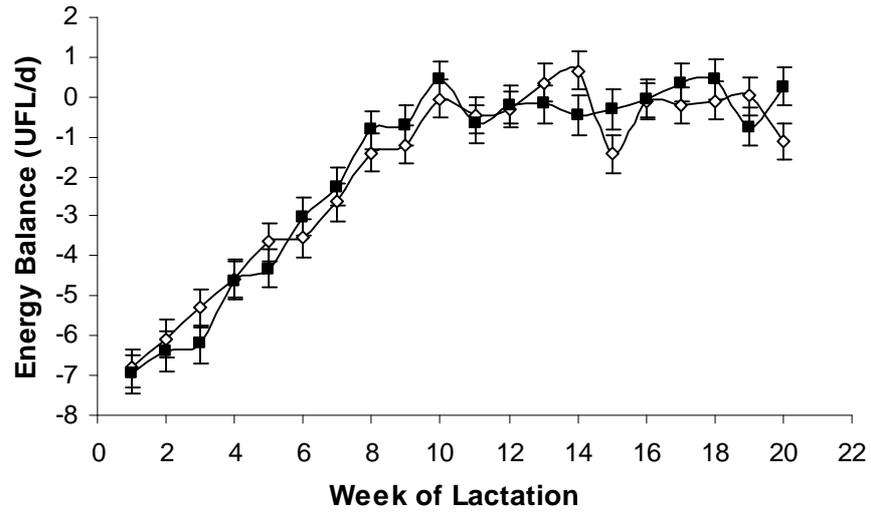
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Figure 2.

699 **Figure 2.** Effect of strain of Holstein-Friesian on dry matter intake (◇ = North American Holstein
700 Friesian; ■ = New Zealand Holstein Friesian). The P-values for the effects of strain, week and
701 interaction between strain and week on daily dry matter intake from wk 1 until wk 20 *post partum* were
702 0.07, <0.001 and 0.90, respectively. The s.e.d. was 0.8 kg/day.



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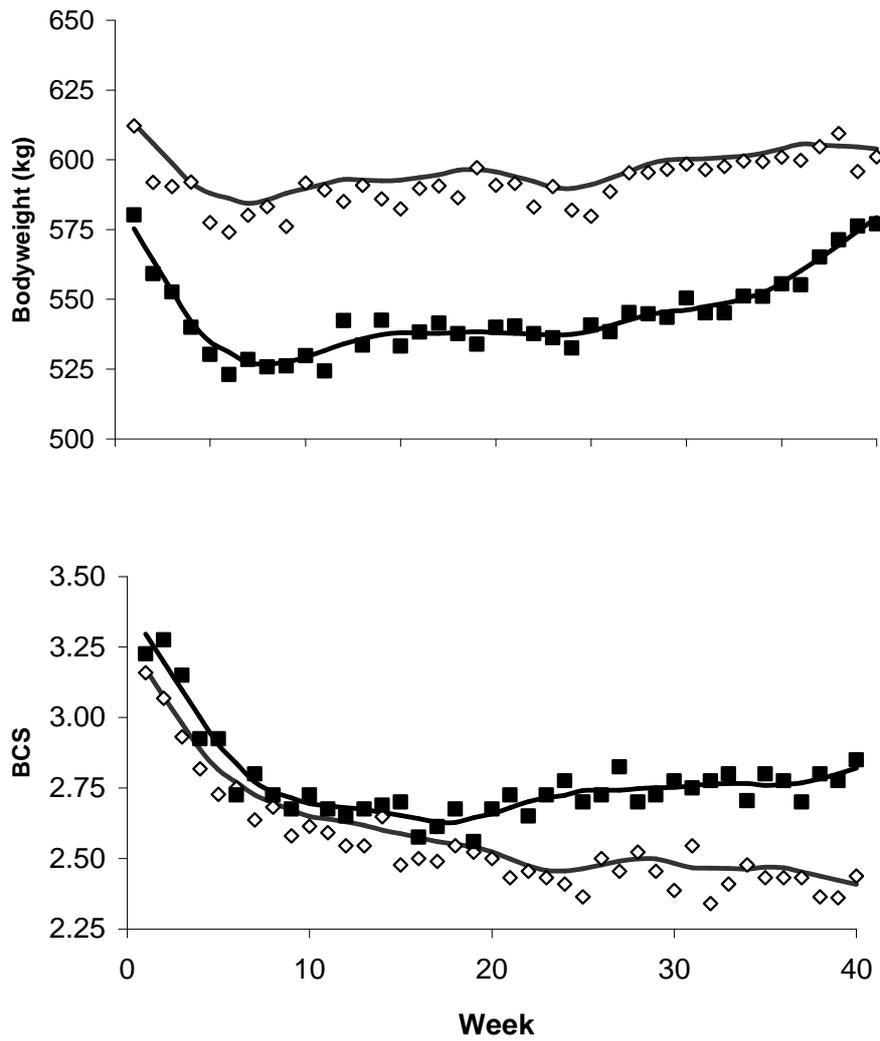
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Figure 3.

720 **Figure 3.** Effect of strain of Holstein-Friesian on energy balance (\diamond = North American Holstein
721 Friesian; \blacksquare = New Zealand Holstein Friesian) from wk 1 to 20 of lactation. The P values for the effects
722 of strain, week and interaction between strain and week were 0.95, <0.001 and 0.94, respectively. The
723 s.e.d. was 0.6 UFL/day.



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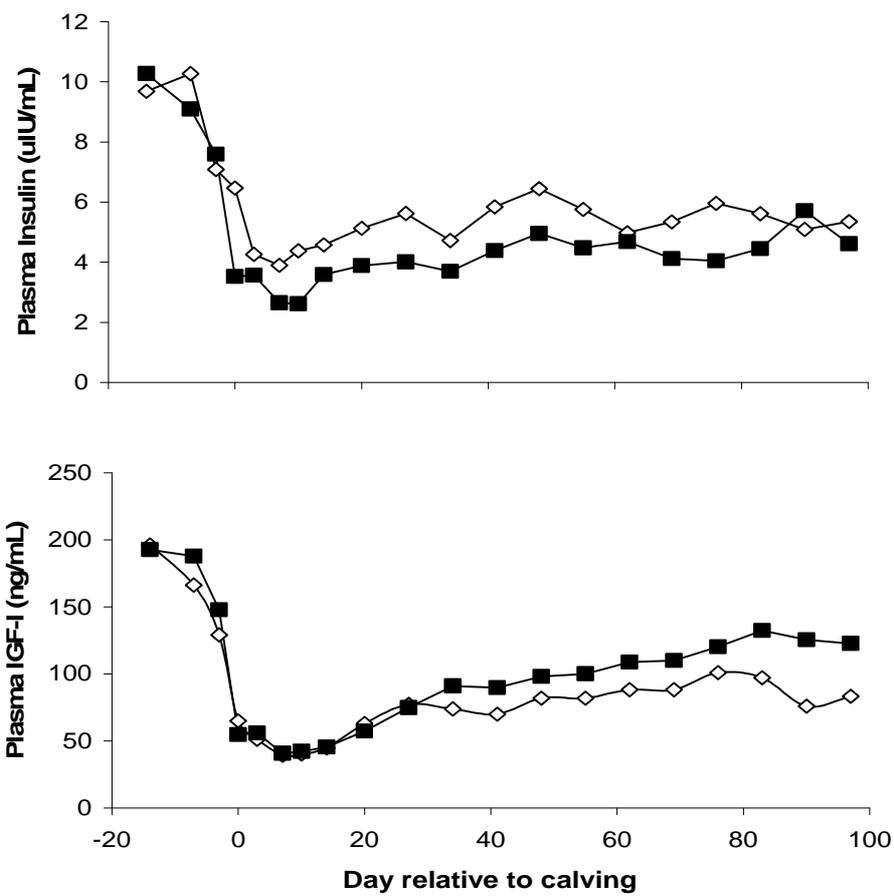
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Figure 4.

735 **Figure 4.** Effect of strain of Holstein-Friesian on body condition score (BCS) and bodyweight (\diamond =
736 North American Holstein Friesian; \blacksquare = New Zealand Holstein Friesian). The P values for the effects of
737 strain, week and interaction between strain and week on weekly BCS were 0.16, <0.001 and 0.009,
738 respectively. The s.e.d. was 0.08 BCS units. The P values for the effects of strain, week and interaction
739 between strain and week on weekly bodyweight were 0.02, <0.001 and 0.57, respectively. The s.e.d.
740 was 15.5 kg. Figures are presented with LOESS-smoothed lines for illustrative purposes.



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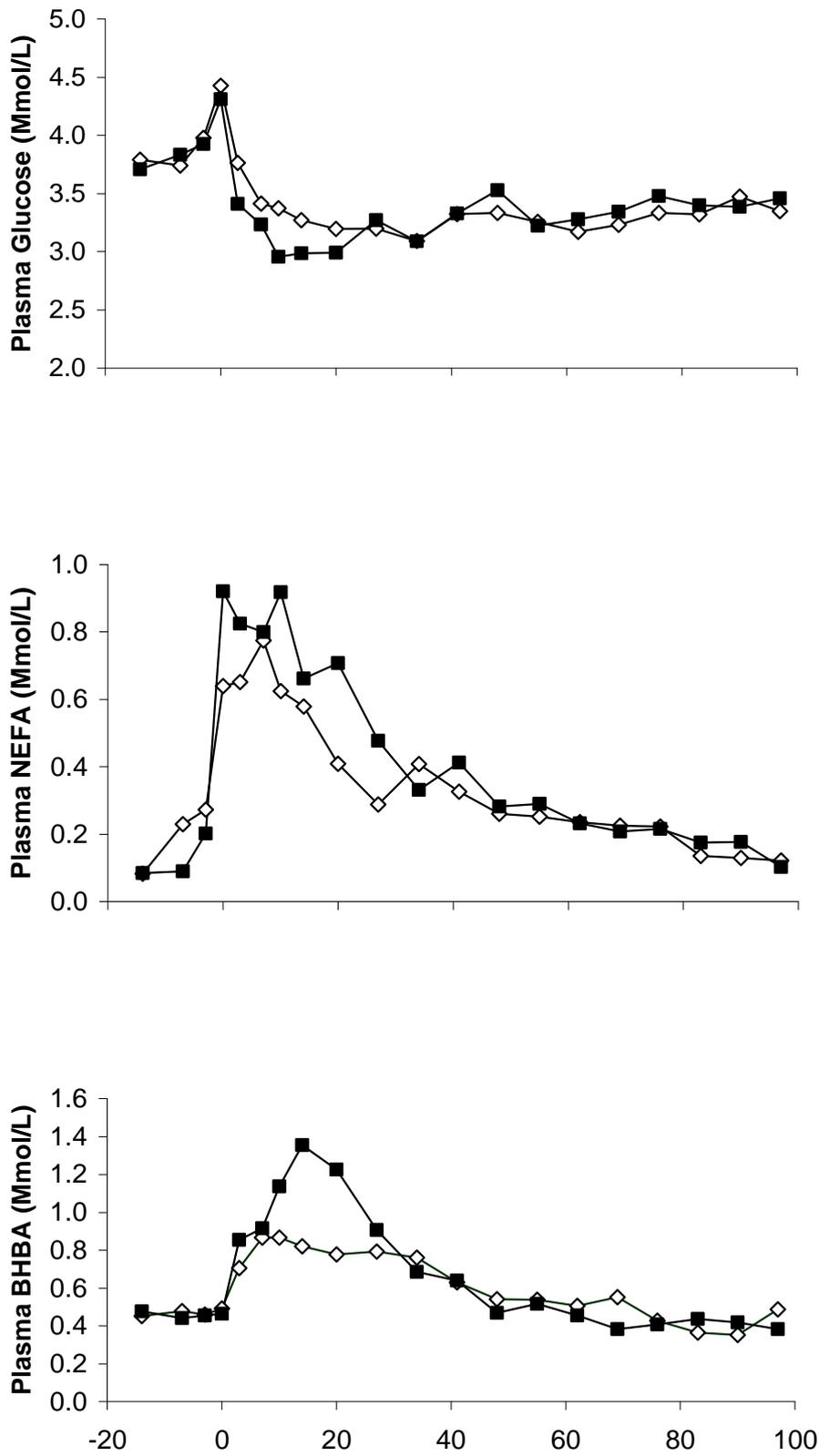
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Figure 5.

753 **Figure 5.** Effect of strain of Holstein-Friesian on plasma insulin and IGF-I concentrations (\diamond = North
754 American Holstein Friesian; \blacksquare = New Zealand Holstein Friesian). The P-values for the effect of strain
755 on insulin concentration were 0.01 and 0.06 for the transition period (2 wk *pre partum* to d 28 *post*
756 *partum*) and post transition period (d 29 to d 100 *post partum*), respectively. The P-values for the effect
757 of strain on IGF-I concentration were 0.71 and 0.04 for the transition and post-transition periods,
758 respectively. There were no significant strain-by-time interactions observed for either insulin or IGF-I
759 across the entire experimental period ($P > 0.05$).

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Figure 6.

763 **Figure 6.** Effect of strain of Holstein-Friesian on plasma glucose, non-esterified fatty acid (NEFA) and
764 beta-hydroxybutyrate concentrations (\diamond = North American Holstein Friesian; \blacksquare = New Zealand
765 Holstein Friesian). The P-values for the effect of strain on glucose concentration were 0.01 and 0.21 for
766 the transition period (2 wk *pre partum* to d 28 *post partum*) and post transition period (d 29 to d 100
767 *post partum*), respectively. The P-values for the effect of strain on NEFA concentration were 0.29 and
768 0.99 for the transition and post-transition periods, respectively. The P-values for the effect of strain on
769 BHBA concentration were 0.02 and 0.45 for the transition and post-transition periods, respectively.
770 There were no significant strain-by-time interactions observed for glucose, NEFA or BHBA
771 concentrations across the entire experimental period ($P > 0.05$).