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Running title: Palm oil and lactating sow diets

**Supplementing sow diets with palm oil during late gestation and
lactation; Effects on milk production, sow hormonal profiles, and growth
and development of her offspring**

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20 **Abstract:** The supplementing of sow diets with lipids during pregnancy and
21 lactation has been shown to reduce sow condition loss and improve piglet
22 performance. The aim of this study was to determine the effects of
23 supplemental palm oil (**PO**) on sow performance, plasma metabolites and
24 hormones, milk profiles, and pre-weaning piglet development. A commercial
25 sow ration (**C**) or an experimental diet supplemented with 10% extra energy in
26 the form of PO, were provided from d 90 of gestation until weaning (24-28 d
27 *post-partum*) in two groups of 8 multiparous sows. Gestation length of PO
28 sows increased by 1 day ($P<0.05$). Maternal body weight changes were
29 similar throughout the trial, but loss of backfat during lactation was reduced in
30 PO animals (C: -3.6 ± 0.8 mm; PO: -0.1 ± 0.8 mm; $P<0.01$). Milk fat was
31 increased by PO supplementation (C d3: $8.0\pm 0.3\%$ fat; PO d3: $9.1\pm 0.3\%$ fat;
32 C d7: $7.8\pm 0.5\%$ fat; PO d7: $9.9\pm 0.5\%$ fat; $P<0.05$) and hence milk energy yield
33 of PO sows was also elevated ($P<0.05$). The proportion of saturated fatty
34 acids was greater in colostrum from PO sows (C: 29.19 ± 0.31 g/100g of fat;
35 PO: 30.77 ± 0.36 g/100g of fat; $P<0.01$). Blood samples taken on 105 days of
36 gestation, within 24 hours of farrowing, day 7 of lactation and at weaning ($28 \pm$
37 3 days post-farrowing) showed there were no differences in plasma
38 concentrations of triacylglycerol, non-esterified fatty acids, insulin or insulin-
39 like growth factor-1 throughout the trial. However, circulating plasma
40 concentrations of both glucose and leptin were elevated during lactation in PO
41 sows ($P< 0.05$ and $P<0.005$, respectively) and thyroxine was greater at
42 weaning in PO sows ($P < 0.05$). Piglet weight and body composition were
43 similar at birth, as were piglet growth rates throughout the pre-weaning period.
44 Seven days after birth, C piglets contained more body fat, as indicated by their

45 lower fat free mass per kg (C: 66.4 ± 0.8 arbitrary units/kg; PO: 69.7 ± 0.8
46 arbitrary unit/kg; $P < 0.01$), but by day 14 of life this situation was reversed (C:
47 65.8 ± 0.6 arbitrary units/kg; PO: 63.6 ± 0.6 arbitrary units/kg; $P < 0.05$).
48 Following weaning, PO sows exhibited an increased ratio of male to female
49 offspring at their subsequent farrowing (C: 1.0 ± 0.3 ; PO: 2.2 ± 0.2 ; $P < 0.05$). We
50 conclude that supplementation of sow diets with PO during late gestation and
51 lactation appears to increase sow milk fat content and hence energy supply to
52 piglets. Furthermore, elevated glucose concentrations in the sow during
53 lactation may be suggestive of impaired glucose homeostasis.

54

55 **Key Words:** Metabolites, Piglets, Body Composition, Milk, Fatty Acids.

56

57 **Implications**

58 Palm oil can be used as an effective energy source in the diets of pregnant
59 and lactating sows, reducing sow body condition loss whilst improving the
60 energy density of milk available to growing piglets. However, despite these
61 benefits the feeding of palm oil during the latter stages of pregnancy also
62 results in changes to glucose and thyroid metabolism. The causes,
63 consequences and longer term implications of these changes are generally
64 unknown and require further investigation.

65

66 **Abbreviations:** Control (C), fat-free mass (FFM), insulin-like growth factor-1
67 (IGF-1), non-esterified fatty acids (NEFA), palm oil (PO), polyunsaturated fatty
68 acids (PUFA), radioimmunoassay (RIA), total-body electrical conductivity
69 analyzing system (TOBEC), Triiodothyronine (T_3) and thyroxine (T_4)

70

71 **Introduction**

72 Nutrient requirements for lactation in sows are met both by dietary
73 sources, and by maternal tissue stores, resulting in mobilization of body
74 reserves and a reduction in maternal fat reserves by the time of weaning
75 (Mullan and Williams, 1989). Anestrous is highly inversely correlated with
76 body weight and backfat at weaning (Mullan and Williams, 1989; Johnston *et*
77 *al.*, 1993); sows with lower body weight and backfat exhibit longer periods of
78 anestrous, thus reducing the efficiency of production. Supplementation of sow
79 diets with fats during late gestation and lactation can be used as a
80 concentrated source of energy, to increase the concentration of fat in
81 colostrum and milk (Quiniou *et al.*, 2008; Tummaruk *et al.*, 2014) and hence,
82 reduce dependence on maternal body stores and subsequent probability of
83 prolonged anestrous (Tantasuparuk *et al.*, 2001).

84 A number of researchers have reported increased rates of weight gain
85 in piglets suckled by sows supplemented with animal fat during lactation
86 (Tilton *et al.*, 1999; Averette *et al.*, 1999). Piglets suckling from sows fed on
87 animal fat also lay down more fat during the pre-weaning period (Tilton *et al.*,
88 1999). The use of such animal by-products, certainly within the European
89 Union, is now restricted, primarily as a consequence of the BSE crisis
90 (Lauridsen *et al.*, 2007) and concerns about traceability, disease and chemical
91 residues. Consequently, alternative sources of fat are of increasing
92 importance and the use of palm oil is one such alternative to the use of animal
93 fats and carries none of the associated risks; although it should be noted that

94 lipid digestibility has been reported to decline with increasing free fatty acid
95 concentration (Rosero *et al.*, 2016).

96 The use of palm oil in the diets of growing and fattening pigs has been
97 reported by Teye *et al.* (2006) who demonstrated that there were no negative
98 effects with regards to piglet performance by the use of palm oil. This group
99 have previously shown that piglets born to mothers supplemented with palm
100 oil during the first half of gestation were heavier and fatter (Laws *et al.*, 2007),
101 whereas Almond *et al.* (2015) reported increased mortality in piglets born to
102 sows fed palm oil throughout gestation. The aim of this study was to evaluate
103 the effects of feeding 10% extra energy, in the form of palm oil, to sows during
104 late gestation and through lactation on plasma metabolites and hormones,
105 reproductive efficiency, neonatal outcome, and their subsequent growth and
106 development.

107

108 **Materials and Methods**

109 *Animals and Diets*

110 All animals used in these studies were maintained at the Pig Research
111 and Development Unit, Imperial College, London and protocols adopted were
112 similar to previous studies conducted by this group (Laws *et al.*, 2009).
113 Experimental procedures were undertaken in accordance with the Animals
114 (Scientific Procedures) Act, 1986 and were licensed by the Home Office (UK).
115 At all stages of life, animals were kept within the guidelines set out by the
116 Department for Environment, Food and Rural Affairs (DEFRA, 2003), and fed
117 commercially available diets to meet nutrient requirements.

118 Sixteen multiparous sows of a commercial genotype (25% Meishan;
119 12.5% Duroc; 62.5% Large White × Landrace), that had been artificially
120 inseminated with pooled semen from Large White boars (P17 2006, JSR
121 Genetics) were entered into the study on day 90 of gestation. Sows were
122 categorized by parity (C 5.7 ± 0.5 ; PO 5.3 ± 0.5) prior to being randomly
123 assigned to one of two dietary treatment groups to ensure that parity was
124 balanced across treatments. Maternal body weight (252 ± 5 kg Mean \pm SEM)
125 and backfat thickness (17 ± 1 mm Mean \pm SEM) at the start of the study was not
126 significantly different between treatments. Sows were assigned randomly to
127 either a control diet or one containing 10% extra energy in the form of a top
128 dressing of palm oil (**PO**) (33.54 MJ/kg; T Quality Ltd, Swindon, UK).
129 Experimental diets were supplied from day 90 of gestation (term \approx 115 days)
130 and consisted of either: i) control (**C**); 3 kg/d of the standard diet (ABN HE sow
131 pellets; ME 13.1 MJ/kg; Crude protein 12.7%; Oil 4.5% ; Fibre 4.8%; Ash
132 5.3%; Vitamin A 10000 (i.u./kg); Vitamin D3 1875 (i.u./kg); Vitamin E 60
133 (i.u./kg); Lysine 0.55%; Copper 21 mg/kg; ABN, Peterborough, UK); or ii) 3
134 kg/d of the standard diet plus 10% extra energy derived from PO (117g/d).
135 After parturition the following lactation diets were supplied: the C lactation diet
136 consisted 6-9 kg/d of the standard lactation pellets (ABN supreme lactation
137 pellets; ME 14.1 MJ/kg; Crude protein 18%; Oil 7.2%; Fibre 4.0%; Ash 5.0%;
138 Vitamin A 10000 (i.u./kg); Vitamin D3 1875 (i.u./kg); Vitamin E 75 (i.u./kg);
139 Lysine 0.95%; Copper 23 mg/kg; ABN, Peterborough, UK), and the PO
140 lactation diet consisted of 6-9 kg/d of the standard lactation pellets plus 10%
141 extra energy derived from palm oil (40 g palm oil per kg of feed). Sows were
142 offered a fixed amount of the appropriate feed daily (3-9 kg/day depending on

143 stage of gestation/lactation); there were no refusals and as a consequence
144 there were no differences in feed intake observed between treatments. Fatty
145 acid compositions of the experimental diets are shown in Table 1. Piglets had
146 ad-libitum access to creep feed (Primary Select; 16.77 MJ/kg ME; 23.5%
147 crude protein; Oil 9%; Fibre 2%; Ash 6.3%; Vitamin A 12500 (iu/kg); Vitamin
148 D3 2000 iu/kg); Vitamin E 250 (iu/kg); Lysine 1.7%; Copper170 mg/kg;
149 Primary Diets Ltd. UK) from day 14 of life.

150

151 *Production Data*

152 On d 90 and d 109 of gestation, and at weaning, sows were restrained
153 in a weigh crate (UHL Products, UK) while their weight and ultrasonic
154 measurements of backfat thickness (Aloka-echo camera 550-500, Aloka Ltd.
155 Japan) were recorded. Backfat thickness was measured level with the head
156 of the last rib, at the P1 (45 mm from the midline) and the P3 (80 mm from the
157 midline) positions. The average of these two values was then calculated to
158 give the P2 value. After farrowing the numbers of piglets born alive, stillborn
159 and mummified and the number of male and female piglets born were
160 recorded. The length of gestation was calculated from the day of
161 insemination. After weaning, 24-28 days post-partum, sows were inseminated
162 at their first oestrus, dates and results of the subsequent farrowing were
163 recorded.

164

165 *Piglet Growth and Composition*

166 Growth performance of all piglets was observed throughout the
167 neonatal period. Body weight and body composition were recorded at birth

168 and at 7, 14 and 21 days post-farrowing. Piglet growth rate was calculated by
169 regression analysis of piglet weight against time. Body composition of all
170 piglets was determined using a total-body electrical conductivity analyzing
171 system (TOBEC, Model-SA3000 EMSCAN/TOBEC, SA-3203, Biotech
172 Instruments Ltd. UK) on d 0, d 7, d 14 and d 21 of life. Body fat and lean
173 mass tissues within an animal exhibit different conductivities. The increased
174 conductivity of fat free mass is attributed to the presence of sodium (Na) and
175 potassium (K), which in association with water exhibit electrical conductivity
176 (EM-SCAN, 1992). When a subject is placed in the electromagnetic field,
177 energy absorbed is a function of the area (A^2), magnetic field strength (B),
178 conduction per unit volume at a specific frequency (c), and a number of
179 constants (k), such that:

180

$$181 \quad E = A^2 \times B \times c \times k \text{ (Mitchell and Scholz, 2001)}$$

182

183 The energy absorption signal produced by the TOBEC is primarily a
184 function of the fat free mass (**FFM**) and is measured as the difference
185 between coil impedance when empty and that with the subject within (EM-
186 SCAN, 1992). As temperature affects electrical conductivity, it was maintained
187 within the range of 18-22°C. Each piglet was positioned identically within a
188 polycarbonate tube and held in place with a plunger to maintain constancy of
189 position. Tube size was selected according to body weight (<3kg – 128 mm;
190 3-5kg – 150 mm; >5kg – 190mm). Piglet FFM per kg was calculated using the
191 equation shown below, as suggested in the TOBEC manufacturer's
192 instructions.

193 FFM (arbitrary units) = $\sqrt{(\text{TOBEC reading} \times \text{Crown-rump-length/piglet}$
194 weight (kg)

195

196 *Milk Composition*

197 Colostrum samples were collected as near to birth as possible (within
198 12 hours of parturition) via milking by hand. Milk samples were collected on d
199 3, d 7, d 14 and d 21 of lactation following intra-muscular administration of 2
200 mL oxytocin (10 i.u./mL; NVS, UK). On each occasion 20 ml of milk were
201 collected (milking by hand) and stored in azide coated sample pots at 4°C
202 prior to analysis for gross milk composition by an automated infrared filtration
203 system, which was conducted by National Milk Records (Harrogate, UK). A
204 1.5 ml milk sample was stored at -80°C prior to lipid extraction and purification
205 by the method of Folch et al. (1957). Total lipid, neutral lipids or phospholipids
206 were saponified and the fatty acids methylated following the method of
207 Lepage and Roy (1984, 1986). Fatty acid methyl esters were separated on a
208 30 m × 0.25 mm Omegawax capillary column (Supelco, Bellefonte PA, USA)
209 and quantified using a Perkin-Elmer gas chromatograph (Autosystem;
210 Norwalk, Conn.) with a hydrogen flame ionization detector. Nitrogen was
211 used as a carrier gas, and the fatty acid methyl esters were compared with
212 purified standards (Sigma Chemical Co., St Louis, MO.) An estimate of the
213 total milk energy was calculated using the equation from Klaver et al. (1981):

214

215 Total energy (MJ/kg) = $0.0042 \times [(92.2 \times \text{fat \% w/w}) + (61.3 \times \text{protein \% w/w})$
216 $+ (35.6 \times \text{lactose \% w/w})]$,

217

218 *Sow Blood Collection and Analyses*

219 Samples of sow blood were collected (approximately 6 hours after the
220 morning feed) into di-sodium EDTA blood tubes (Teklab, UK) from the jugular
221 vein at 105 days of gestation, within 24 hours of farrowing, day 7 of lactation
222 and at weaning (28 ± 3 days post-farrowing). Although all blood samples
223 were taken within 6 hours of feed being offered, it is important to note that sow
224 feed intake behaviour (irrespective of treatment) was not consistent around
225 the time of parturition. Blood samples were centrifuged for 15 minutes at
226 $1600g_{av}$ (Sci Quip 3K15, Sigma laboratory centrifuges, Osterode am Harz,
227 Germany); plasma was collected and stored at -20°C until analysis. Plasma
228 was analyzed for concentrations of glucose, non-esterified fatty acids (**NEFA**)
229 and triacylglycerol (**TAG**), insulin-like growth factor 1 (**IGF-1**), insulin, thyroid
230 hormones (Triiodothyronine (**T₃**) and thyroxine (**T₄**)) and Leptin using
231 commercially available kits (glucose (GOD-PAP), and triacylglycerol (GPO-
232 PAP) from Randox Laboratories Ltd. UK; NEFA C from Wako Chemical
233 GmbH, Germany; IGF-1 IRMA from Diagnostic Systems Laboratories Inc.,
234 Webster, Texas, USA; Insulin, **T₃** and **T₄** radioimmunoassay (**RIA**) kits from
235 ICN Pharmaceuticals, New York, USA; and leptin RIA assay kit from LINCO
236 Research, St. Charles, Missouri, USA). Intra- and inter- assay Coefficients of
237 Variation for insulin were 5.8 and 2.3%, respectively, 7.9 and 4.9%,
238 respectively for IGF-1, 6.8 and 2.7%, respectively for leptin, 8.3 and 2.5%,
239 respectively for **T₄**, 8.8 and 2.5%, respectively for **T₃**, 4.1 and 2.2%,
240 respectively for glucose, 7.6 and 1.4%, respectively for NEFA, and 4.1 and
241 1.4%, respectively for TAG.

242

243 *Statistical Analyses*

244 Statistical differences between dietary treatments were determined by
245 repeated measures using the mixed model procedure of SAS version 9.4
246 (SAS Institute Inc. Cary, NC, USA). Sources of variation within the model
247 included diet (1 df), sample point (3 df for plasma hormones and 4 df for milk
248 fatty acid analysis) with respect to each specific measure as previously
249 described) and first order interactions between diet and sample point. Parity
250 and litter size were used as covariates; parity was used as a covariate rather
251 than class due to the spread and limited replication within and between
252 treatments with respect to parity number. Individual animal was the repeated
253 subject and sample point the repeated measure. Results are presented as
254 least squares means with standard error and P value. Tukey's simultaneous
255 tests were used to establish statistical difference between means (sample
256 points and first order interactions). Probability values of less than 0.05 were
257 considered to be statistically significant.

258 Individual piglet growth rate was calculated by regression analysis of
259 piglet weight against time. Analysis was conducted for the period between
260 birth and weaning. The slope of the line gave a measure of their growth rate
261 in kg /d.

262

263 **Results**

264 Sow weight change during gestation and lactation were similar, irrespective of
265 treatment. No differences were observed in backfat at the P2 position during
266 gestation, however mean backfat losses were lower in PO sows during
267 lactation (C -3.6 ± 0.8 mm; PO -0.1 ± 0.8 mm; $P < 0.05$). Mean natural

268 gestation length was increased by 1 d for sows in the PO group (C 117 ± 0.3
269 days; PO 118 ± 0.3 days; $P < 0.05$). There were no significant differences in
270 total litter size (mean \pm SEM: 11.5 ± 1.2), number of piglets born alive,
271 stillborn or mummified or in the ratio of male to female piglets. In the
272 subsequent reproductive cycle, weaning to service interval, percentage of
273 successful inseminations, gestation length, litter size and number of piglets
274 born alive, stillborn and mummified were similar for both treatment groups.
275 However, in the subsequent litter the ratio of male to female piglets was two-
276 fold higher in litters born to PO sows compared to C sows (C 1.0 ± 0.3 ; PO 2.2
277 ± 0.2 ; male:female; $P < 0.05$).

278 There were no differences in piglet body weight, either at birth or
279 throughout the neonatal period (Table 2) and consequently piglet growth rates
280 were also similar (C 0.43 ± 0.04 kg/day, PO 0.47 ± 0.04 kg/day; mean \pm SEM).
281 All piglets became fatter with increasing age ($P < 0.05$), as indicated by their
282 lower FFM/kg (Table 2). There were no differences in FFM/kg at birth, but by
283 d 7 of life piglets born to C sows were fatter ($P < 0.01$). In contrast, by d 14, the
284 piglets of PO sows were fatter ($P < 0.05$) but by d 21 no differences existed in
285 piglet FFM between treatments, which may in part be due to the introduction
286 of creep feed on d14.

287 There was no difference in the concentration of milk protein or lactose,
288 but percentage of fat was increased in the milk of sows in the PO group,
289 during the first week of lactation ($P < 0.05$; Table 3); this trend continued to day
290 21 of lactation ($P < 0.1$). As a consequence of the increased proportion of fat in
291 the milk, energy yield was also found to be higher ($P < 0.05$; Table 3). As
292 expected, the addition of palm oil to the maternal diet influenced the fatty acid

293 profile of both colostrum and milk, but only significant treatment differences
294 are highlighted below. The percentage of saturated fatty acids was elevated
295 in the colostrum of PO sows ($P<0.01$; Table 4). On day 3 of lactation the
296 proportion of eicosadienoic (20:2 n-6) acid was lower in the milk of PO sows
297 ($P<0.01$; Table 4). During mid-lactation (days 7 and 14) the percentage of
298 myristoleic (14:1) acid was decreased in the milk of PO sows ($P<0.05$; Table
299 4). Similarly, by day 21 of lactation the proportion of α -linolenic acid (18:3 n-3)
300 acid was reduced in the milk of PO sows ($P<0.05$; Table 4). There were
301 effects of time on fatty acid profile such that the sum of saturates increased
302 between subsequent sample points ($P<0.05$), the sum of monounsaturated
303 fatty acids increased between 0 and 3 days post-partum and then remained
304 similar. Conversely the sum of polyunsaturated fatty acids (**PUFA**), n-6, n-3
305 and the PUFA to saturated ratio declined over successive sample points.
306 There were no interactions between diet and sample point.

307 There were no effects of PO on plasma concentrations of TAG, NEFA,
308 insulin and IGF-1 at any time point (Table 5). Concentrations of glucose were
309 greater in the PO group during lactation ($P<0.05$) as were concentrations of
310 leptin ($P<0.005$), although these effects did not persist into weaning (Table 5).
311 Concentrations of T_3 were greater in the PO group at weaning ($P<0.05$)
312 although there were no effects of treatment or time point on concentrations of
313 T_4 (Table 5). Circulating concentrations of IGF-1 were seen to increase with
314 each successive time point ($P<0.001$) but these changes were not related to
315 diet. There were no interactions between diet and sample point for any of the
316 parameters determined in sow plasma (Table 5).

317

318 **Discussion**

319 *Maternal Performance*

320 Feeding animal fat during gestation has been shown to increase weight
321 gain in sows (Avarette *et al.*, 2002), while the addition of fat to the lactation
322 diet did not appear to influence maternal weight loss (Averette *et al.*, 1999). In
323 the present study, neither weight gain during the last few weeks of pregnancy
324 nor weight loss during lactation were affected by supplementation of sow diets
325 with palm oil, which may be in part due to the timing and duration of fat
326 supplementation. However, it should be noted that replication was limited and
327 statistical differences may have been masked by variation due to the small
328 number of animals in each group. Consequently care needs to be exercised
329 when interpreting these results.

330

331 During gestation, sow backfat has been shown to increase linearly with
332 increasing feed intake (Dourmad, 1991; Cools *et al.*, 2014) but this was not
333 reflected in the current study. However, during lactation, backfat loss was
334 lower in the PO group, which is in accordance with the findings of others
335 (Tilton *et al.*, 1999; Avarette *et al.*, 2002). This apparent reduction in sow
336 backfat loss at weaning could have been a result of increased dietary energy
337 intake during lactation.

338

339 Avarette *et al.* (2002) found no difference in the gestational length of sows
340 after supplementation with either medium or long chain (animal fat)
341 triacylglycerols. Conversely, in the present study supplementation of the
342 maternal diet with PO during the last few weeks of gestation was observed to

343 increase gestational length by one day. The review of Tanghe and De Smet
344 (2013) into the effects of maternal fatty acid supplementation indicated that
345 the effects that supplementary PUFA had on gestational length were not
346 consistent. These authors suggested that the effects reported on gestational
347 length may be a consequence of PUFA induced changes to eicosanoid
348 production, or alterations to enzymes involved in steroid hormone production.

349 The sex-allocation hypothesis of Triver and Willard (1973) predicts that
350 females in the best body condition will tend to produce offspring of the gender
351 which favours the sex of greater variance (i.e. males). This hypothesis has
352 been supported by observations in several species (Rosenfeld and Roberts,
353 2004), including pigs (Meikle *et al.*, 1996). In this experiment the subsequent
354 litter of PO sows contained a higher proportion of male offspring, which may
355 reflect the energy status of sows at the time of insemination/implantation.
356 Rosenfeld *et al.*, (2003) observed similar results in mice fed either a high
357 saturated fat or high carbohydrate diet; however, the mechanisms for diet-
358 induced skewing of sex ratio is not known, but a number of possible
359 mechanisms have been suggested and are discussed in a review by
360 Rosenfeld and Roberts (2004).

361

362 *Plasma Metabolites and hormones*

363 It is well known that NEFA are a product of fat metabolism and a sign of
364 catabolism of fat reserves. There were no effects of PO supplementation on
365 circulating concentrations of NEFA at any time during the present study, which
366 could reflect the minimal change in net backfat thickness. The net reduction in
367 backfat depth of C sows during lactation might have been anticipated to result

368 in increased circulating concentrations of NEFA (Ren *et al.*, 2017) but
369 surprisingly this was not the case in the current study.

370 Glucose concentrations were higher in the plasma of PO sows on day
371 7 of lactation. This reflects the findings of van der Peet-Schwering *et al.*
372 (2004) who reported increased glucose concentrations in fat supplemented
373 sows during lactation. These authors suggested that elevated glucose
374 concentrations were a consequence of fat induced glucose intolerance, as
375 sows fed an isocaloric diet containing starch did not exhibit the same
376 alterations in glucose concentration. Within the current study the elevated
377 concentrations of glucose in PO sows during lactation appear to coincide with
378 higher circulating concentrations of insulin, although differences in circulating
379 concentrations of insulin failed to achieve statistical significance. This might
380 be indicative of insulin resistance/glucose intolerance as Almond *et al.* (2015)
381 reported increased area under the curve following a glucose tolerance test in
382 late gestation in sows supplemented with palm oil. Furthermore, they also
383 reported a higher incidence of piglet mortality in palm oil supplemented sows,
384 which was attributed to birth hypoglycemia. These authors proposed that
385 maternal glucose intolerance resulted in impaired piglet cognition at birth
386 leading to reduced suckling activity and hence increased incidence of
387 hypoglycemia at birth. The elevated glucose and insulin concentrations
388 recorded in the current study occurred during lactation rather than during
389 pregnancy and so were unlikely to affect piglet glycaemic status and
390 subsequent mortality.

391 Circulating concentrations of leptin were also found to be higher in PO
392 sows on day 7 of lactation. Leptin is mainly produced by adipocytes and

393 adipose tissue and circulating concentrations of leptin are linked to body
394 stores (Summer *et al.*, 2009). A number of studies have shown a direct
395 correlation with levels of sow adiposity and circulating concentrations of leptin
396 (Estienne *et al.*, 2000; De Rensis *et al.*, 2005; Summer *et al.*, 2009). This is
397 reflected in the current study whereby both PO and C sows gained similar
398 levels of backfat during gestation but during lactation body stores were
399 maintained in PO sows but reduced in C sows.

400 Although circulating concentrations of T₄ were not appreciably different
401 between treatments or time points in the current study, those of T₃ were seen
402 to be higher in PO supplemented sows, particularly at weaning (P<0.05). This
403 mirrors the findings of Von Eder and Kirchgessner (1997) who reported that
404 circulating T₄ concentrations were not influenced by lipid supplementation but
405 T₃ concentrations were increased when soya oil and olive oil were lipid
406 sources, but the same effect was not apparent when beef fat was the source.
407 These authors concluded that fat source rather than fat content influenced
408 thyroid hormone metabolism.

409

410 *Milk Composition*

411 In the current study milk from PO sows contained more fat whereas
412 protein and lactose concentrations were similar, irrespective of the maternal
413 diet. These observations are in agreement with other published research,
414 which found that protein and lactose concentrations varied little with dietary
415 supplementation with animal fat (Shurson, 1986) or other lipid sources
416 (Lauridsen and Danielsen, 2004). However, Lauridsen and Danielsen (2004)
417 also went on to report that the addition of different fats and oils to sow diets

418 did not alter the total lipid content of milk. This disparity in findings between
419 these authors' and those of the current study may reflect the higher levels of
420 dietary fat used in the current study.

421 The higher fat percentage observed in the milk of PO animals resulted
422 in a greater energy yield per kg of milk produced. The increased percentage
423 of saturated fatty acids in the colostrum (day 0) of PO sows echoes the
424 elevated saturated fatty acid content of the maternal diet (Table 1). Previous
425 research has shown that milk fatty acid composition mirrors that of the
426 maternal diet (Lauridsen and Danielsen, 2004). However, there were no diet
427 induced differences in milk total saturates throughout the rest of lactation
428 despite the differences observed in the total saturates of the lactation diet.

429 Lauridsen and Danielsen (2004) reported elevated levels of palmitic
430 acid in the milk of sows offered diets containing palm oil. The same effect
431 was not apparent in the present study, where there were no diet related
432 differences in the C16:0 content of milk at any time point despite the much
433 higher levels of C16:0 in the PO diet. There were some small transitory
434 differences in milk fatty acids 14:1, 18:3, 20:2 between diets, but these were
435 not consistent and followed no discernable pattern over the course of
436 lactation. The effects of time with respect to changes in milk total saturates,
437 monounsaturates and PUFA seen in the current study have been reported
438 previously (Skrzypczak et al., 2015) and are typical of changes seen in
439 porcine milk fat profiles with advancing stage of lactation.

440

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442 In the present study birth weight of piglets were unaffected by
443 manipulation of the maternal diet during late gestation. This is in agreement
444 with findings of others following the provision of additional energy as fats
445 during the latter stages of gestation (Seerley *et al.*, 1978; Quiniou *et al.*,
446 2008). However, Wang *et al.* (2016) reported a linear increase in piglet size
447 with increasing energy provision during pregnancy, although it should be
448 noted that total litter weight was not appreciably different between treatments.

449 In this trial piglet body composition (as indicated by FFM/kg) was also
450 shown to be similar between treatments at birth. By d 7 of life, piglets sucking
451 from C sows contained more fat, but by d 14 of life, piglets sucking from PO
452 animals were the fattest (as indicated by their lower FFM/kg). The variation in
453 body composition between birth and weaning between groups may be due to
454 differences in milk yield and individual piglet suckling behavior. Previous
455 studies have shown that piglets reared by sows receiving fat supplements
456 during lactation grew faster; the composition of the increased weight gain was
457 almost exclusively fat (Tilton *et al.*, 1999).

458

459 **Conclusions**

460 Results from this study suggests that the increase in energy intake by
461 the sow, associated with palm oil supplementation, appears to alter milk
462 composition, which may in turn influence early postnatal growth, development
463 and body composition of suckling piglets. Elevated glucose concentrations in
464 the sow seen during lactation may be suggestive of impaired glucose
465 homeostasis. However, due to the limited replication within the current study

466 care needs to be exercised when interpreting data and as such further work is
467 required in this area.

468

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475

476 **Declaration of Interest**

477 The authors declare that they have no conflict of interest

478 **Ethics Statement**

479 The study was subject to local ethical review and conducted in accordance
480 with Imperial College's animal research policy and all procedures were
481 conducted and conformed to the United Kingdom's Animal (Scientific
482 Procedures) Act 1986.

483 **Software and data repository sources**

484 Data and models are not available in an official repository

485

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619 performance, and milk fat and protein output. *Livestock Science*. 194: 23-30.

620

621 **Table 1:** Fatty acid composition of sow diets

	Gestation diet		Lactation diet	
	Control	Palm Oil	Control	Palm Oil
12:O	ND	ND	0.26	0.15
14:O	0.53	0.80	0.85	0.90
15:O	0.09	0.15	ND	ND
16:O	18.24	28.07	20.45	25.58
16:1 (n-7)	0.32	0.40	0.24	0.21
17:1	0.08	0.08	0.07	0.09
18:O	3.14	3.73	5.22	5.32
18:1 (n-9)	19.98	29.35	32.81	35.80
18:2 (n-6)	50.33	33.46	34.83	28.88
18:3 (n-3)	4.76	2.93	3.97	1.71
20:0	ND	ND	0.53	0.47
20:1 (n-9)	0.66	0.46	0.36	0.54
20:2 (n-6)	0.25	0.08	ND	ND
20:3 (n-3)	0.04	ND	ND	ND
20:4 (n-6)	ND	ND	0.01	0.01
20:5 (n-3)	0.35	0.12	0.30	0.27
22:O	0.65	0.15	0.00	0.00
22:1 (n-9)	0.38	0.13	0.00	0.00
22:5 (n-3)	ND	0.10	0.00	0.00
22:6 (n-3)	0.21	ND	0.08	0.07
ΣS	22.65	32.90	27.31	32.43
ΣM	21.34	30.34	33.48	36.63
ΣP	55.94	36.68	39.21	30.94
Σn-6	50.58	33.54	34.84	28.90
Σn-3	5.36	3.15	4.36	2.04
P:S	2.47	1.11	1.44	0.95
n-6 :n-3	9.45	10.66	7.99	14.13

622

623 S = saturated fatty acids; M = monounsaturated fatty acids; P = Poly-unsaturated fatty acids;

624 ND = none detected. Values presented are mean percentages from 2 determinations of total

625 lipid fraction extracted from samples of diet

626

627

628 **Table 2:** Effect of maternal diet on piglet weight (kg) and fat-free mass/kg
 629 (FFM/kg)¹

Day ²	Weight (kg)		FFM/kg (arbitrary units)	
	C ³	PO ³	C	PO
0	1.64±0.04	1.61±0.04	79.1±0.9	77.9±0.9
7	2.91±0.08	2.91±0.08	66.4±0.8**	69.7±0.8**
14	4.79±0.12	5.05±0.12	65.8±0.6*	63.6±0.6*
21	6.91±0.17	6.72±0.17	60.2±0.7	61.1±0.7

630

631 ¹ Data are presented as adjusted least squares means ± SEM (parity and litter size were
 632 analyzed as co-variates)

633 ² Day of life (birth on day 0)

634 ³ C= Control diet, PO = Palm oil diet.

635 * Denotes significant differences (*: $P < 0.05$; **: $P < 0.01$) between treatments (C vs. PO) in
 636 FFM/kg

637

638 **Table 3:** Effect of maternal diet on sow milk composition and milk energy¹

Day ³	Fat %		Protein %		Lactose %		Energy (MJ/kg) ²	
	C ⁴	PO	C	PO	C	PO	C	PO
3	8.0±0.3*	9.1±0.3*	4.8±0.2	4.9±0.2	5.4±0.1	5.1±0.1	5.70±0.25	5.64±0.25
7	7.8±0.5*	9.9±0.5*	5.0±0.4	4.6±0.4	5.2±0.4	5.2±0.4	4.99±0.15**	5.84±0.15**
14	8.1±0.5	8.5±0.5	4.4±0.1	4.7±0.1	5.7±0.1	5.5±0.1	5.06±0.15	5.34±0.15
21	7.0±0.4	8.4±0.4	4.6±0.2	4.6±0.2	5.5±0.1	5.4±0.1	4.69±0.16*	5.24±0.18*

639

640 ¹ Data are presented as adjusted least squares means ± SEM641 ² MJ/kg of milk, MJ calculated as 0.0042 x (92.2 x fat + 61.3 x protein + 35.6 x lactose)642 ³ Days since parturition643 ⁴ C= Control diet, PO = Palm oil diet.644 * Denotes significant differences (*: $P < 0.05$; **: $P < 0.01$) between treatments (C vs. PO) within
645 each milk fraction.

646
647

Table 4: Mean effects of sow diet during late gestation and lactation on the fatty acid profile (g/100g fatty acid) of their colostrum and milk over a 21 day lactation.

Fatty Acid	Day 0		Day 3		Day 7		Day 14		Day 21		P-value	
	C	PO	C	PO	C	PO	C	PO	C	PO	Diet	Day
14:0	1.47±0.16	0.35±0.18	2.15±0.24	2.37±0.24	2.99±0.21	2.84±0.21	3.32±0.27	2.77±0.27	3.25±0.20	2.83±0.20	0.097	<0.001
14:1	0.03±0.04	0.02±0.01	0.11±0.03	0.13±0.03	0.20±0.03*	0.09±0.03*	0.24±0.04*	0.08±0.04*	0.20±0.04	0.09±0.04	0.001	0.003
16:0	22.1±0.40	23.4±0.47	26.1±1.21	29.2±1.21	31.3±1.32	29.9±1.32	33.6±1.74	32.4±1.74	34.7±1.45	33.6±1.45	0.618	<0.001
16:1(n-7)	3.24±0.55	3.47±0.63	6.29±0.67	7.92±0.67	8.94±0.90	7.47±0.90	9.77±1.04	7.64±1.04	10.22±0.81	8.26±0.81	0.066	<0.001
18:0	5.46±0.27	5.68±0.31	5.76±0.33	4.86±0.33	5.11±0.32	5.14±0.32	4.72±0.35	4.74±0.35	4.32±0.27	4.59±0.27	0.745	<0.001
18:1(n-9)	35.8±1.25	35.7±1.45	38.2±1.19	35.5±1.19	31.8±1.68*	34.8±1.68*	30.5±2.04	33.7±2.04	29.6±1.55	33.3±1.55	0.048	0.002
18:2(n-6)	26.0±1.28	24.3±1.47	16.9±0.76	16.0±0.76	15.6±0.77	15.8±0.77	14.4±0.86	15.2±0.86	14.3±0.57	14.0±0.57	0.761	<0.001
18:3(n-6)	0.37±0.04	0.24±0.05	0.05±0.04	0.08±0.04	0.04±0.02	0.05±0.02	0.03±0.01	0.02±0.01	0.04±0.02	0.03±0.02	0.370	<0.001
18:3(n-3)	1.46±0.25	1.69±0.29	1.13±0.05	1.03±0.05	1.20±0.08	1.13±0.08	1.14±0.08	1.07±0.08	1.11±0.05*	0.96±0.05*	0.050	0.003
20:1(n-9)	0.32±0.06	.21±0.06	0.39±0.04	0.35±0.07	0.33±0.07	0.34±0.07	0.35±0.10	0.32±0.06	0.32±0.07	0.29±0.07	0.416	0.262
20:2(n-6)	0.52±0.08	.47±0.09	0.57±0.05**	0.28±0.05**	0.42±0.06	0.33±0.06	0.31±0.07	0.29±0.07	0.33±0.05	0.26±0.05	0.049	0.007
20:4(n-6)	1.07±0.09	1.01±0.11	0.83±0.07	0.79±0.07	0.65±0.04	0.64±0.04	0.48±0.04	0.51±0.04	0.45±0.03	0.44±0.03	0.702	<0.001
20:5(n-3)	0.24±0.11	0.25±0.13	0.43±0.11	0.30±0.11	0.38±0.03	0.46±0.31	0.26±0.07	0.32±0.07	0.45±0.14	0.46±0.14	0.177	<0.001
22:1(n-9)	0.10±0.04	0.12±0.04	0.09±0.02	0.12±0.02	0.11±0.01	0.09±0.01	0.07±0.02	0.10±0.02	0.08±0.02	0.10±0.02	0.437	0.761
22:2(n-6)	0.05±0.22	0.44±0.25	ND	0.01±0.00	0.06±0.03	0.01±0.03	0.01±0.00	0.01±0.00	0.01±0.00	0.01±0.00	0.167	0.087
22:5(n-3)	0.43±0.05	0.34±0.06	0.32±1.03	0.29±0.03	0.24±0.03	0.26±0.03	0.21±0.02	0.19±0.02	0.20±0.02	0.17±0.02	0.177	<0.001
22:6(n-3)	0.33±0.05	0.32±0.06	0.22±0.02	0.24±0.02	0.02±0.03	0.18±0.03	0.17±0.03	0.14±0.03	0.16±0.03	0.12±0.03	0.662	<0.001
∑S	29.2±0.31**	30.8±0.36**	34.2±1.24	36.7±1.24	39.7±1.36	39.7±1.36	41.9±1.82	40.2±1.82	42.5±1.44	41.3±1.44	0.049	<0.001
∑M	39.6±1.58	39.6±1.83	45.1±0.82	44.1±0.82	41.4±1.20	42.9±1.20	40.9±1.46	41.9±1.46	40.4±0.97	42.1±0.97	0.276	0.001
∑P	31.1±1.52	29.6±1.75	20.6±0.93	19.2±0.93	19.2±0.93	18.9±0.90	18.9±0.90	17.1±0.98	17.8±0.74	16.6±0.74	0.735	<0.001
∑n-6	28.8±1.37	27.2±1.58	18.7±0.85	17.6±0.85	17.1±0.82	17.1±0.82	15.5±0.88	16.24±0.88	15.3±0.66	15.0±0.66	0.577	<0.001
∑n-3	2.61±0.24	2.73±0.28	2.12±0.12	1.93±0.12	2.04±0.32	2.03±0.32	1.79±0.12	1.73±0.12	1.93±0.20	1.74±0.20	0.733	<0.001
P:S	1.06±0.05	0.96±0.06	0.61±0.04	0.54±0.04	0.48±0.04	0.50±0.04	0.41±0.04	0.46±0.04	0.40±0.03	0.41±0.03	0.735	<0.001
n-6:n-3	12.4±1.48	10.0±1.71	8.99±0.41	9.19±0.41	8.60±0.74	9.28±0.74	8.72±0.39	9.55±0.39	8.31±0.81	9.18±0.81	0.798	0.032

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C= Control diet, PO = Palm oil diet; S = saturated fatty acids; M = monounsaturated fatty acids; P = Poly-unsaturated fatty acids; ND= none detected;

Data presented are adjusted least squares means ± SEM, Tukey's test was used to determine differences between treatment means.

* Denotes significant differences (*: $P<0.05$; **: $P<0.01$) between treatments (C vs. PO) within each sample time point.

652 **Table 5:** Effect of sow diet on circulating concentrations of leptin, insulin, insulin-like growth factor-1 (IGF-1), T₃, T₄, glucose and
 653 lipids

Sample time	105d Gestation		Farrowing ¹		Lactation ¹		Weaning ¹		P-values	
	C	PO	C	PO	C	PO	C	PO	Diet	Time
Glucose (mM)	4.47±0.28	4.26±0.29	4.36±0.42	5.14±0.24	4.69±0.28*	5.41±0.26*	4.96±0.29	5.02±0.32	0.049	0.125
TAG (mM)	0.31±0.09	0.37±0.09	0.33±0.12	0.23±0.09	0.31±0.09	0.26±0.09	0.33±0.09	0.55±0.10	0.805	0.097
NEFA (mM)	0.22±0.05	0.21±0.05	0.34±0.07	0.29±0.05	0.24±0.05	0.36±0.05	0.18±0.05	0.27±0.06	0.588	0.075
Leptin (ng/ml)	3.29±0.41	4.14±0.42	3.10±0.84	3.79±0.42	2.94±0.45***	5.02±0.42***	3.24±0.41	4.34±0.46	0.035	0.774
Insulin (µIU/ml)	44.2±10.14	30.6±9.92	39.0±15.12	29.6±9.32	40.7±9.73	57.7±9.64	44.3±9.73	37.3±11.04	0.701	0.540
IGF-1 (ng/ml)	180±96.5	145±112.4	275±121.3	252±113.1	358±109.4	387±112.7	373±109.4	396±114.3	0.995	<0.001
T ₃ (ng/ml)	0.45±0.51	0.63±0.52	0.55±0.76	1.85±0.53	0.55±0.51	1.09±0.52	0.66±0.52*	2.40±0.53*	0.049	0.065
T ₄ (ng/ml)	30.9±1.83	32.2±1.88	24.1±2.73	30.5±1.90	29.4±1.83	32.7±1.88	31.7±1.83	33.7±1.98	0.514	0.485

654 ¹ Sample time: Farrowing = within 24 hours of parturition; Lactation = d7 of lactation; Weaning = d 28±3 of lactation)
 655 C= Control diet, PO = Palm oil diet, TAG = Triacylglycerol, NEFA = Non esterified fatty acid, IGF-1 = Insulin-like growth factor 1, T₃ = Triiodothyronine, T₄ =
 656 thyroxine.
 657 * Denotes significant differences (*: $P<0.05$; **: $P<0.01$; ***: $P<0.005$) between treatments (C vs. PO) within each sample time point.