

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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1	Running title: Palm oil and lactating sow diets
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4	lactation; Effects on milk production, sow hormonal profiles, and growth
5	and development of her offspring
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Abstract: The supplementing of sow diets with lipids during pregnancy and 20 21 lactation has been shown to reduce sow condition loss and improve piglet 22 The aim of this study was to determine the effects of performance. 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 the form of PO, were provided from d 90 of gestation until weaning (24-28 d 26 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±0.3% fat; PO d3: 9.1±0.3% fat; 32 C d7: 7.8±0.5% fat; PO d7: 9.9±0.5% fat; P<0.05) and hence milk energy yield of PO sows was also elevated (P<0.05). The proportion of saturated fatty 33 34 acids was greater in colostrum from PO sows (C: 29.19±0.31 g/100g of fat; PO: 30.77±0.36 g/100g of fat; P<0.01). Blood samples taken on 105 days of 35 gestation, within 24 hours of farrowing, day 7 of lactation and at weaning (28 ± 36 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 weaning in PO sows (P < 0.05). Piglet weight and body composition were 42 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: 65.8 ± 0.6 arbitrary units/kg; PO: 63.6 ± 0.6 arbitrary units/kg; P<0.05). 47 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.

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

56

57 Implications

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

65

Abbreviations: Control (C), fat-free mass (FFM), insulin-like growth factor-1
 (IGF-1), non-esterified fatty acids (NEFA), palm oil (PO), polyunsaturated fatty
 acids (PUFA), radioimmunoassay (RIA), total-body electrical conductivity
 analyzing system (TOBEC), Triiodothyronine (T₃) and thyroxine (T₄)

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 reserves and a reduction in maternal fat reserves by the time of weaning 74 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 prolonged anestrous (Tantasuparuk et al., 2001). 83

84 A number of researchers have reported increased rates of weight gain in piglets suckled by sows supplemented with animal fat during lactation 85 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., 1999). The use of such animal by-products, certainly within the European 88 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 Consequently, alternative sources of fat are of increasing residues. 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).

The use of palm oil in the diets of growing and fattening pigs has been 96 97 reported by Teye et al. (2006) who demonstrated that there were no negative effects with regards to piglet performance by the use of palm oil. This group 98 99 have previously shown that piglets born to mothers supplemented with palm oil during the first half of gestation were heavier and fatter (Laws et al., 2007), 100 101 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 similar to previous studies conducted by this group (Laws et al., 2009). 112 113 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; 12.5% Duroc; 62.5% Large White × Landrace), that had been artificially 119 inseminated with pooled semen from Large White boars (P17 2006, JSR 120 121 Genetics) were entered into the study on day 90 of gestation. Sows were categorized by parity (C 5.7 \pm 0.5; PO 5.3 \pm 0.5) prior to being randomly 122 123 assigned to one of two dietary treatment groups to ensure that parity was 124 balanced across treatments. Maternal body weight (252±5 kg Mean±SEM) 125 and backfat thickness (17±1mm Mean±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) and consisted of either: i) control (C); 3 kg/d of the standard diet (ABN HE sow 130 131 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 kg/d of the standard diet plus 10% extra energy derived from PO (117g/d). 134 135 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); Lysine 0.95%; Copper 23 mg/kg; ABN, Peterborough, UK), and the PO 139 lactation diet consisted of 6-9 kg/d of the standard lactation pellets plus 10% 140 141 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 stage of gestation/lactation); there were no refusals and as a consequence
there were no differences in feed intake observed between treatments. Fatty
acid compositions of the experimental diets are shown in Table 1. Piglets had
ad-libitum access to creep feed (Primary Select; 16.77 MJ/kg ME; 23.5%
crude protein; Oil 9%; Fibre 2%; Ash 6.3%; Vitamin A 12500 (iu/kg); Vitamin
D3 2000 iu/kg); Vitamin E 250 (iu/kg); Lysine 1.7%; Copper170 mg/kg;
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. Japan) were recorded. Backfat thickness was measured level with the head 155 156 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 give the P2 value. After farrowing the numbers of piglets born alive, stillborn 158 and mummified and the number of male and female piglets born were 159 160 recorded. The length of gestation was calculated from the day of insemination. After weaning, 24-28 days post-partum, sows were inseminated 161 162 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 regression analysis of piglet weight against time. Body composition of all 169 170 piglets was determined using a total-body electrical conductivity analyzing system (TOBEC, Model-SA3000 EMSCAN/TOBEC, SA-3203, 171 Biotech Instruments Ltd. UK) on d 0, d 7, d 14 and d 21 of life. Body fat and lean 172 173 mass tissues within an animal exhibit different conductivities. The increased conductivity of fat free mass is attributed to the presence of sodium (Na) and 174 175 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 $E = A^2 \times B \times c \times k$ (Mitchell and Scholz, 2001)

182

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

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 12 hours of parturition) via milking by hand. Milk samples were collected on d 198 199 3, d 7, d 14 and d 21 of lactation following intra-muscular administration of 2 mL oxytocin (10 i.u./mL; NVS, UK). On each occasion 20 ml of milk were 200 201 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 1.5 ml milk sample was stored at -80°C prior to lipid extraction and purification 204 205 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 Lepage and Roy (1984, 1986). Fatty acid methyl esters were separated on a 207 208 30 m × 0.25 mm Omegawax capillary column (Supelco, Bellefonte PA, USA) and quantified using a Perkin-Elmer gas chromatograph (Autosystem; 209 210 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 purified standards (Sigma Chemical Co., St Louis, MO.) An estimate of the 212 213 total milk energy was calculated using the equation from Klaver et al. (1981):

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215 Total energy (MJ/kg) = 0.0042 × [(92.2 × fat % w/w) + (61.3 × protein % w/w)
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+ (35.6 × lactose % w/w)],

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218 Sow Blood Collection and Analyses

Samples of sow blood were collected (approximately 6 hours after the 219 220 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 and at weaning $(28 \pm 3 \text{ days post-farrowing})$. Although all blood samples 222 223 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 1600gav (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 hormones (Triiodothyronine (T_3) and thyroxine (T_4)) and Leptin using 230 commercially available kits (glucose (GOD-PAP), and triacylglycerol (GPO-231 PAP) from Randox Laboratories Ltd. UK; NEFA C from Wako Chemical 232 233 GmbH, Germany; IGF-1 IRMA from Diagnostic Systems Laboratories Inc., Webster, Texas, USA; Insulin, T₃ and T₄ radioimmunoassay (RIA) kits from 234 235 ICN Pharmaceuticals, New York, USA; and leptin RIA assay kit from LINCO Research, St. Charles, Missouri, USA). Intra- and inter- assay Coefficients of 236 237 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%, respectively for glucose, 7.6 and 1.4%, respectively for NEFA, and 4.1 and 240 241 1.4%, respectively for TAG.

243 Statistical Analyses

244 Statistical differences between dietary treatments were determined by repeated measures using the mixed model procedure of SAS version 9.4 245 246 (SAS Institute Inc. Cary, NC, USA). Sources of variation within the model included diet (1 df), sample point (3 df for plasma hormones and 4 df for milk 247 248 fatty acid analysis) with respect to each specific measure as previously described) and first order interactions between diet and sample point. Parity 249 250 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.

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

262

263 **Results**

Sow weight change during gestation and lactation were similar, irrespective of treatment. No differences were observed in backfat at the P2 position during gestation, however mean backfat losses were lower in PO sows during lactation (C -3.6 \pm 0.8 mm; PO -0.1 \pm 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 days; PO 118± 0.3 days; P<0.05). There were no significant differences in 269 270 total litter size (mean \pm SEM: 11.5 \pm 1.2), number of piglets born alive, 271 stillborn or mummified or in the ratio of male to female piglets. In the subsequent reproductive cycle, weaning to service interval, percentage of 272 273 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 2.2277 ± 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 were also similar (C 0.43±0.04 kg/day, PO 0.47±0.04 kg/day; mean±SEM). 280 All piglets became fatter with increasing age (P<0.05), as indicated by their 281 282 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 piglets of PO sows were fatter (P<0.05) but by d 21 no differences existed in 284 285 piglet FFM between treatments, which may in part be due to the introduction of creep feed on d14. 286

There was no difference in the concentration of milk protein or lactose, but percentage of fat was increased in the milk of sows in the PO group, during the first week of lactation (P<0.05; Table 3); this trend continued to day 21 of lactation (P<0.1). As a consequence of the increased proportion of fat in the milk, energy yield was also found to be higher (P<0.05; Table 3). As 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 in the colostrum of PO sows (P<0.01; Table 4). On day 3 of lactation the 295 296 proportion of eicosadienoic (20:2 n-6) acid was lower in the milk of PO sows (P<0.01; Table 4). During mid-lactation (days 7 and 14) the percentage of 297 298 myristoleic (14:1) acid was decreased in the milk of PO sows (P<0.05; Table 4). Similarly, by day 21 of lactation the proportion of α -linolenic acid (18:3 n-3) 299 300 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 and the PUFA to saturated ratio declined over successive sample points. 305 306 There were no interactions between diet and sample point.

307 There were no effects of PO on plasma concentrations of TAG, NEFA, insulin and IGF-1 at any time point (Table 5). Concentrations of glucose were 308 309 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 T₄ (Table 5). Circulating concentrations of IGF-1 were seen to increase with each successive time point (P<0.001) but these changes were not related to 314 315 diet. There were no interactions between diet and sample point for any of the parameters determined in sow plasma (Table 5). 316

318 **Discussion**

319 Maternal Performance

Feeding animal fat during gestation has been shown to increase weight 320 321 gain in sows (Avarette et al., 2002), while the addition of fat to the lactation diet did not appear to influence maternal weight loss (Averette et al., 1999). In 322 323 the present study, neither weight gain during the last few weeks of pregnancy nor weight loss during lactation were affected by supplementation of sow diets 324 325 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

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

338

Avarette *et al.* (2002) found no difference in the gestational length of sows after supplementation with either medium or long chain (animal fat) triacylglycerols. Conversely, in the present study supplementation of the maternal diet with PO during the last few weeks of gestation was observed to increase gestational length by one day. The review of Tanghe and De Smet (2013) into the effects of maternal fatty acid supplementation indicated that the effects that supplementary PUFA had on gestational length were not consistent. These authors suggested that the effects reported on gestational length may be a consequence of PUFA induced changes to eicosanoid production, or alterations to enzymes involved in steroid hormone production.

The sex-allocation hypothesis of Triver and Willard (1973) predicts that 349 350 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 reflect the energy status of sows at the time of insemination/implantation. 355 356 Rosenfeld et al., (2003) observed similar results in mice fed either a high 357 saturated fat or high carbohydrate diet; however, the mechanisms for dietinduced skewing of sex ratio is not known, but a number of possible 358 mechanisms have been suggested and are discussed in a review by 359 Rosenfeld and Roberts (2004). 360

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

Glucose concentrations were higher in the plasma of PO sows on day 370 371 7 of lactation. This reflects the findings of van der Peet-Schwering et al. (2004) who reported increased glucose concentrations in fat supplemented 372 373 sows during lactation. These authors suggested that elevated glucose concentrations were a consequence of fat induced glucose intolerance, as 374 375 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 be indicative of insulin resistance/glucose intolerance as Almond et al. (2015) 380 381 reported increased area under the curve following a glucose tolerance test in 382 late gestation in sows supplemented with palm oil. Furthermore, they also reported a higher incidence of piglet mortality in palm oil supplemented sows, 383 which was attributed to birth hypoglycemia. These authors proposed that 384 385 maternal glucose intolerance resulted in impaired piglet cognition at birth leading to reduced suckling activity and hence increased incidence of 386 387 hypoglycemia at birth. The elevated glucose and insulin concentrations 388 recorded in the current study occurred during lactation rather than during pregnancy and so were unlikely to affect piglet glycemic status and 389 390 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 adipose tissue and circulating concentrations of leptin are linked to body stores (Summer *et al.*, 2009). A number of studies have shown a direct correlation with levels of sow adipocity and circulating concentrations of leptin (Estienne *et al.*, 2000; De Rensis *et al.*, 2005; Summer *et al.*, 2009). This is reflected in the current study whereby both PO and C sows gained similar levels of backfat during gestation but during lactation body stores were maintained in PO sows but reduced in C sows.

400 Although circulating concentrations of T_4 were not appreciably different 401 between treatments or time points in the current study, those of T₃ were seen to be higher in PO supplemented sows, particularly at weaning (P<0.05). This 402 403 mirrors the findings of Von Eder and Kirchgessner (1997) who reported that 404 circulating T₄ concentrations were not influenced by lipid supplementation but T₃ concentrations were increased when soya oil and olive oil were lipid 405 sources, but the same effect was not apparent when beef fat was the source. 406 407 These authors concluded that fat source rather than fat content influenced thyroid hormone metabolism. 408

409

410 Milk Composition

In the current study milk from PO sows contained more fat whereas protein and lactose concentrations were similar, irrespective of the maternal diet. These observations are in agreement with other published research, which found that protein and lactose concentrations varied little with dietary supplementation with animal fat (Shurson, 1986) or other lipid sources (Lauridsen and Danielsen, 2004). However, Lauridsen and Danielsen (2004) also went on to report that the addition of different fats and oils to sow diets did not alter the total lipid content of milk. This disparity in findings between
these authors' and those of the current study may reflect the higher levels of
dietary fat used in the current study.

421 The higher fat percentage observed in the milk of PO animals resulted in a greater energy yield per kg of milk produced. The increased percentage 422 423 of saturated fatty acids in the colostrum (day 0) of PO sows echoes the elevated saturated fatty acid content of the maternal diet (Table 1). Previous 424 425 research has shown that milk fatty acid composition mirrors that of the 426 maternal diet (Lauridsen and Danielsen, 2004). However, there were no diet induced differences in milk total saturates throughout the rest of lactation 427 428 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 was not apparent in the present study, where there were no diet related 431 432 differences in the C16:0 content of milk at any time point despite the much higher levels of C16:0 in the PO diet. There were some small transitory 433 differences in milk fatty acids 14:1, 18:3, 20:2 between diets, but these were 434 not consistent and followed no discernable pattern over the course of 435 436 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 previously (Skrzypczak et al., 2015) and are typical of changes seen in 438 porcine milk fat profiles with advancing stage of lactation. 439

440

441 Growth and Development of Offspring

In the present study birth weight of piglets were unaffected by manipulation of the maternal diet during late gestation. This is in agreement with findings of others following the provision of additional energy as fats during the latter stages of gestation (Seerley *et al.*, 1978; Quiniou *et al.*, 2008). However, Wang *et al.* (2016) reported a linear increase in piglet size with increasing energy provision during pregnancy, although it should be 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 from C sows contained more fat, but by d 14 of life, piglets sucking from PO 451 452 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 differences in milk yield and individual piglet suckling behavior. Previous 454 455 studies have shown that piglets reared by sows receiving fat supplements 456 during lactation grew faster; the composition of the increased weight gain was almost exclusively fat (Tilton et al., 1999). 457

458

459 **Conclusions**

Results from this study suggests that the increase in energy intake by the sow, associated with palm oil supplementation, appears to alter milk composition, which may in turn influence early postnatal growth, development and body composition of suckling piglets. Elevated glucose concentrations in the sow seen during lactation may be suggestive of impaired glucose 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 is467 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**

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

483 **Software and data repository sources**

484 Data and models are not available in an official repository

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Table 1: Fatty acid composition of sow diets 621

	Gestat	ion diet	Lactat	ion 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
22:0	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
∑n-6	50.58	33.54	34.84	28.90
∑n-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;

ND = none detected. Values presented are mean percentages from 2 determinations of total 624 625 lipid fraction extracted from samples of diet

626

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

629 (FFM/kg)¹

	Weigł	nt (kg)	FFM/kg (arbitrary units)			
Day ²	C ³	PO ³	С	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

Energy (MJ/kg)² Fat % Protein % Lactose % C^4 С С Day³ PO С PO PO 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*

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

639

640 ¹ Data are presented as adjusted least squares means ± SEM

641 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 parturition

643 ⁴C= Control diet, PO = Palm oil diet.

^{*} Denotes significant differences (*: *P*<0.05; **: *P*<0.01) between treatments (C vs. PO) within

645 each milk fraction.

Table 4: Mean effects of sow diet during late gestation and lactation on the fatty acid profile (g/100g fatty acid) of their colostrum 646 647 and milk over a 21 day lactation.

Eatty Acid	Day 0		Day 3		Day 7		Day 14		Day 21		P-value	
Fatty Acid	С	PO	С	PO	С	PO	С	PO	С	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 [*]	$0.08 \pm 0.04^{*}$	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 [*]	$0.96 \pm 0.05^{*}$	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
ΣS	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
ΣM	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
ΣP	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

648

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. 649

* Denotes significant differences (*: P<0.05; **: P<0.01) between treatments (C vs. PO) within each sample time point. 650

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	
	С	PO	С	PO	С	PO	С	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/mI)	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
T₃ (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	$0.66 \pm 0.52^{*}$	2.40±0.53*	0.049	0.065
T₄ (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

¹Sample time: Farrowing = within 24 hours of parturition; Lactation = d7 of lactation; Weaning = d 28±3 of lactation)

C = Control diet, PO = Palm oil diet, TAG = Triacylglycerol, NEFA = Non esterified fatty acid, IGF-1 = Insulin-like growth factor 1, T₃ = Triiodothyronine, T₄ = thyroxine.

657 * Denotes significant differences (*: *P*<0.05; **: *P*<0.01; ***: *P*<0.005) between treatments (C vs. PO) within each sample time point.