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Metabolic and hormonal effects of whole grains of rye, oats and wheat in dog food

Hanna Palmqvist[†,‡,*], Sara Ringmark[‖], Johan Dicksved[‡], Torbjörn Lundh[‡], and Katja Höglund[‖]

[†]Department of Clinical Sciences, Faculty of Veterinary Medicine and Animal Science, Swedish University of Agricultural Sciences, 750 07, Uppsala, Sweden
[‡]Department of Applied Animal Science and Welfare, Faculty of Veterinary Medicine and Animal Science, Swedish University of Agricultural Sciences, 750 07, Uppsala, Sweden
[‖]Department of Animal Biosciences, Faculty of Veterinary Medicine and Animal Science, Swedish University of Agricultural Sciences, 750 07, Uppsala, Sweden

*Corresponding author: hanna.palmqvist@slu.se

Abstract

Inclusion of whole grains in the diet of humans has been shown to improve the postprandial metabolic response and is considered to promote health and prevent certain diseases. Less is known about effects of different whole grains on the metabolic response in dogs. The objective of the present study was to investigate and compare the metabolic and hormonal response in dogs fed extruded diets containing whole grains from rye, oat or wheat, three commonly grown cereals in the Nordic countries. The study was performed in a cross-over design using 18 healthy adult privately-owned dogs. Three extruded experimental diets were produced containing whole grain flour of either rye (RYE), wheat (WHE) or ground rolled oats (OAT) at 25% inclusion level. The diets were nutritionally complete and comparable in terms of protein and metabolizable energy content. Each diet was fed for 4 wk, with blood sampling on the last day of each period (fasting sample followed by post-prandial samples at 20, 40, 60, 120, 180, and 240 min). The resulting number of repetitions per diet was: WHE: $n = 16$, OAT: $n = 17$, RYE: $n = 17$. The blood samples were analyzed to determine glucose, insulin, glucagon-like peptide-1 (GLP-1), glucagon, triacylglycerol (TAG) and cholesterol concentrations. There were no main effects of diet on postprandial blood response curves and no effect of interaction of diet and time for any of the variables analyzed. Evaluation of area under the curve (AUC) showed higher total concentration following the OAT than WHE diet for glucose ($P = 0.035$), GLP-1 ($P = 0.006$) as well as TAG ($P = 0.025$). Fasting insulin concentration was higher following RYE compared with both other diets ($P = 0.005$), but there were no differences in insulin AUC between the diets. In the early postprandial phase (0–120 min), there was an overall effect of diet on the ratio of insulin to GLP-1 ($P = 0.042$). Post hoc test was not significant, but the WHE diet resulted in a numerically higher value than the other two diets. In conclusion, the postprandial response curves were in general similar between the diets and imply that, in dogs, whole rye or oats may not be more beneficial than whole wheat.

Lay Summary

The health promoting effects of including whole grains in the diet of humans are well known. However, the capacity to lower blood glucose and lipids seems to differ between different whole grains, with oats and rye showing beneficial effects more frequently than wheat. In dogs these effects are less studied, but could be of importance given the increasing problems with overweight and obesity in companion dogs. In this study, diets with whole grains of rye, oats or wheat were fed for 4 wk each to 18 privately-owned dogs. Blood response of glucose, lipids (cholesterol and triglycerids [TAG]) and three hormones related to metabolism (insulin, glucagon and glucagon-like peptide 1 [GLP-1]) were measured in blood samples collected from the dogs both in the fasted state and repeatedly during four hours following a meal. The diet with oats resulted in higher concentration of GLP-1, which regulates the metabolism, but had less favorable effects on blood glucose and lipid levels, compared to the diet with wheat. The fasting insulin concentration was highest following the rye diet. These results imply that, in dogs, whole rye or oats may not be favorable compared with whole wheat.

Key words: glucagon like peptide-1, glucose, insulin, postprandial, privately-owned, triacylglycerol

Abbreviations: AUC, area under curve, BW, body weight, DM, dry matter, FFA, free fatty acid receptor, GLP-1, glucagon-like peptide 1, SCFA, short-chain fatty acid, SLU, Swedish University of Agricultural Sciences, TAG, triacylglycerol

Introduction

Inclusion of whole grains in the diet has long been considered to promote good health in humans, lowering the risk of developing diseases such as type II diabetes mellitus and cardiovascular disease (Aune et al., 2016). Compared with refined foods, whole-grain products have been shown in several human studies to improve postprandial glycemia and insulinaemia and to lower blood cholesterol (Hollænder et al., 2015; Marventano et al., 2017; Sanders et al., 2023). In commercial dog food the major carbohydrate source is often refined, contributing mostly starch. However, the potential benefits of including dietary fiber in dog food are gaining increasing attention (Kayser et al. 2024). Specific fiber types with different fermentability potential have been studied in dogs, with conflicting results regarding glucose, insulin, cholesterol, and the incretin glucagon-like peptide-1 (GLP-1) (Massimino et al., 1998; Bosch et al., 2009;

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Alexander et al., 2018; Ferreira et al., 2018). Studies comparing metabolic effects of different whole grains in diets for dogs are scarce and those performed to date have not observed similar effects on glycaemic control as seen in humans (Kempe et al., 2008; Traughber et al., 2021). There are some studies on use of other carbohydrate sources in dog diets (Carciofi et al., 2008; Rankovic et al., 2020), with varying results, but overall indicating that diets high in dietary fiber can attenuate the glycaemic response.

In the Nordic countries, wheat, rye, and oats are the most commonly grown and consumed cereals in humans (Frølich et al., 2013). Oats contain the viscous fiber beta-glucan, which increases the viscosity of the digesta in the intestine, thereby slowing glucose uptake and trapping cholesterol-containing bile acids, which are then eliminated via the feces (McRorie and McKeown, 2017). Whole grain rye is rich in the less viscous fiber arabinoxylan, but has also been shown to have beneficial effects on glycaemic control in humans and pigs by decreasing the need for insulin compared with a control (often refined wheat bread) (Leinonen et al., 1999; Juntunen et al., 2003; Rosen et al., 2009; Theil et al., 2011). Whole wheat also contains arabinoxylan, but of a less soluble type than rye arabinoxylan (Knudsen, 2014), and thus could have differing effects on metabolism compared with rye.

To the best of our knowledge, metabolic effects of rye have not been studied previously in dogs. Wheat and oats are used as ingredients in dog food, but use of rye is very uncommon. In previous studies, we have shown that fecal microbiota composition and function in a cohort of dogs fed different whole grains (Palmqvist et al., 2023a), or whole grain rye compared with refined wheat (Palmqvist et al., 2023b), were affected in ways that could be beneficial to metabolic health. Given the scarcity of studies comparing metabolic effects of different whole grains in dogs, we decided to investigate this potential benefit further. The objective of the present study was therefore to investigate and compare the metabolic and hormonal response in dogs fed extruded diets containing whole grains from rye, oat or wheat. Our hypothesis was that the diets containing rye or oat would result in more stable concentration of blood glucose and insulin as well as higher GLP-1, compared with the diet containing wheat.

Material and Methods

The study was approved by the Ethics Committee for Animal Experiments, Uppsala, Sweden (Approval no. 5.8.18-18808/2017-7), and was performed in compliance with ARRIVE guidelines (Percie du Sert et al., 2020). The experiment was carried out in the period August-December 2019 in a cross-over design. Eighteen dogs owned by staff and students at the Swedish University of Agricultural Sciences (SLU) in Uppsala, Sweden, were enrolled. All dogs lived in their home environment during the study. Examinations and sampling of the dogs were performed at SLU. All dog owners gave written informed consent before the start of the study. Information from owners was handled in accordance with General Data Protection Regulation (Regulation [EU] 2016/679).

Diets

The three extruded experimental diets used in the study were produced by Doggy AB, Vårgårda, Sweden. The diets contained whole grain flour of either rye (RYE), wheat (WHE) or ground rolled oats (OAT) at 25% inclusion level, as-fed (Table 1). The diets were nutritionally complete and balanced according to European Pet Food Industry Federation (FEDIAF, 2019) and formulated to be similar in protein and metabolizable energy content (Table 2). The diets were indistinguishable to humans in terms of appearance, odor and texture and the packaging were all white.

Animals

An e-mail invitation to volunteer dogs for participation in the study was sent to staff and students at SLU and at the University Animal Hospital in Uppsala, Sweden. For inclusion in the study, dogs had to be ≥12 mo of age, weigh ≥7 kg and be deemed healthy based on the following clinical investigations: physical examination (performed by the same veterinarian [HP] on all dogs), routine hematology, serum biochemical analyses

Table 1. Ingredients in the three experimental diets, expressed as % included

Ingredient	Wheat diet	Oat diet	Rye diet
Wheat flour	25.0	—	—
Oat flour	—	25.0	—
Rye flour	—	—	25.0
Maize	15.0	15.0	15.0
Rice	11.7	12.5	10.8
Lignocellulose[1]	1.5	1.5	1.5
Dried chicken meal	29.7	29.9	30.4
Fresh chicken meat	5.0	5.0	5.0
Chicken stock[2]	3.0	3.0	3.0
Pork fat	7.5	6.4	7.6
Premix of minerals and vitamins[3]	1.7	1.7	1.7

[1]Source of insoluble fiber consisting of lignin, cellulose and hemicellulose.
[2]Source of flavor.
[3]Nutrients added per kg: Vitamin A (IE) 11100, Vitamin D3 (IE) 1160, Vitamin E (mg) 299, Vitamin C (mg) 403, thiamin B1 (mg) 2.9, Riboflavin B2 (mg) 4, Pyridoxine B6 (mg) 2, Niacin B3 (mg) 19.9, Pantothenic acid B5 (mg) 17.6, Biotin (mg) 0.2, Vitamin B12 (mg) 0.06, Folic acid (mg) 0.4, Copper(II) sulphate pentahydrate (mg) 23, Copper (mg) 6, Manganese(II) oxide/manganese(III) oxide (mg) 9.6, Manganese (mg) 5.8, Zinc sulphate monohydrate (mg) 101, Zinc (mg) 36, Calcium iodate anhydrate (mg) 17.8, and Iodine (mg) 1.8.

Table 2. Analyzed chemical composition of the experimental diets, expressed as % of dry matter (DM) unless otherwise stated

Item	Wheat diet	Oat diet	Rye diet
Dry matter	93.9	93.5	93.9
Gross energy, MJ/kg DM	20.9	21.7	21.5
Metabolizable energy, MJ/kg DM[1]	17.2	18.0	17.8
Organic matter	92.9	93.1	92.7
Crude protein	30.5	30.4	29.5
Crude fat	13.7	17.6	16.7
Crude fiber	1.9	1.5	1.8
Total dietary fiber	8.6	7.6	9.1
Soluble dietary fiber	1.4	2.0	1.7
Insoluble dietary fiber	7.2	5.6	7.4
Total starch	38.3	34.2	34.8
Resistant starch	0.2	0.2	0.3
Non-resistant starch	38.1	34.0	34.5
Acid-insoluble ash	0.06	0.06	0.05

[1]Calculated based on crude fiber in accordance with National Research Council (2006).

(parameters of liver and kidney function and C-reactive protein [CRP]) and urine analysis (standard dipstick chemistry test, urine specific gravity and protein per creatinine ratio). Dogs that had been treated with antibiotics within 3 mo prior to the study, were allergic or had known intolerance to any of the experimental food ingredients or a history of sensitivity to diet change were excluded. Initially, 22 dogs were recruited. However, four dogs had problems with loose stools, signs of possible cutaneous adverse food reaction or palatability issues during acclimatization to the diets or early in the first experimental diet period, and were hence excluded in agreement with their owners. The remaining 18 dogs comprised 13 purebreds (two dogs of the same breed) and five dogs of mixed breeds (Supplementary Table S1). Mean ± SD age was 5.7 ± 2.6 yr, mean ± SD body condition score (BCS) on a 9-point scale (Laflamme, 1997) was 5.2 ± 0.6 and mean ± SD body weight (BW) was 18.4 ± 9.5 kg.

All 18 dogs completed all study periods except one dog, which died during the last diet period. Post-mortem analysis determined that this death occurred for reasons unrelated to the study. Five dogs were treated with non-steroidal anti-inflammatory (NSAID) medication for at least one short period during the study, for reasons unrelated to the study. One dog was treated for a localized skin infection with an ointment containing betamethasone and fucidic acid during the last diet period. The skin infection had unknown etiology but was healed by the medical treatment and did not recur after completion of treatment, which ended 3 wk prior to the last sampling day. The results for that dog's samples did not deviate from results of samples collected previously from the same dog, and hence they were included in the statistical analysis.

Study design

The cross-over design took the form of a reduced 3 × 3 Latin square, with diet order WHE-OAT-RYE, OAT-RYE-WHE and RYE-WHE-OAT. Participating dogs were categorized by sex and size (Supplementary Table S1), anonymized and randomly divided into three similarly composed groups. The three diet orders were then randomly assigned to these groups. Pairs of dogs living in the same household were assigned to the same dog group. There were three such pairs, which were randomized to different groups. All owners were blinded to diets and diet order. Each dog's normal caloric intake before the study was used as reference to calculate a start daily feed allowance. Owners were instructed to weigh their dog on the same scale once a week during the study period. The daily caloric allowance was adjusted by the research team to maintain original BW. The owners were instructed to keep their dog's normal feeding routines. Treats were allowed as long as the experimental diet was the main source of energy and as long as the treats were given in approximately the same amount during each diet period. However, owners were instructed to give nothing but the experimental diet during the last 3 d before sampling in each diet period.

In order to make the starting conditions as similar as possible for all dogs, they were all first fed the WHE diet for 3 wk, including a 4–7 d transition period for acclimatization, before starting the first experimental diet period. During the transition period, the owners were instructed to mix the dog's normal food with the WHE diet in increasing amounts. Each experimental diet was then fed for 4 wk and thereafter followed by the next diet, with a transition period of 4–7 d. After each diet period, the owners were asked to fill out a questionnaire about their dog's digestive functions and appetite behavior (Supplementary Questionnaire S2).

Blood sampling and handling

On the last day of each experimental diet period, the dogs were fasted overnight and brought to the examination clinic at SLU for sample collection. On arrival at the clinic, each dog was weighed and a peripheral vein catheter (BD Venflon, New Jersey, United States) was placed in the cephalic vein. A fasting blood sample was collected and then the dog was offered half of its daily caloric allowance of the current experimental diet. The postprandial period started when the dog started to eat. Blood samples were then collected at 20, 40, 60, 120, 180, and 240 min postprandially. The vein catheter was flushed with 1 mL saline solution after each sampling. Prior to each sampling, 0.5–1 mL was drawn with a syringe from the catheter and discarded, to avoid sample dilution.

For analysis of cholesterol, triacylglycerol (TAG) and glucagon, 4 mL of blood was collected in Vacuette serum clot activator tubes (Greiner Bio-One GmbH, Kremsmünster, Austria) and allowed to clot at room temperature for a minimum of 30 min before centrifugation at 2,000 g for 10 min at 4 °C. For analysis of glucose, insulin and total GLP-1, 2 mL of blood was collected in BD Vacutainer tubes (BD, New Jersey, United States) containing K2 EDTA as anticoagulant and kept on ice until centrifugation at 2,000 g for 10 min at 4 °C, which was performed within 45 min. After centrifugation, aliquots of serum and plasma were transferred to cryotubes and kept at −80°C until further analysis.

Analysis of metabolic and hormonal response

All analyses of metabolic and hormonal parameters in blood samples were performed in accordance with the manufacturers' instructions, by laboratory staff who were blinded to dog identity and diet. Hormone (insulin, glucagon and GLP-1) and glucose analyses were performed at the Department of Applied Animal Science and Welfare, SLU, Uppsala, Sweden. The samples were analyzed in duplicate and the mean of the two results was used in data analysis. Serum glucagon concentration was analyzed using a human enzyme-linked immunosorbent assay (ELISA) kit (Mercodia, Uppsala, Sweden) previously validated for dogs (Söder et al., 2016). Concentration of plasma insulin was analyzed using a canine-specific ELISA kit (Mercodia, Uppsala Sweden). For analysis of plasma glucose concentration, the samples were diluted 1:10 before analysis using an enzymatic UV-method (D-glucose; Boehringer Mannheim, Germany) previously used in dogs (Hesta et al., 2001). Mean intra-assay coefficient of variation (CV) for the glucagon, insulin and glucose assays were 3.1%, 2.2%, and 2.4%, respectively. Concentrations of total cholesterol and TAG in serum were analyzed at the Department of Clinical Chemistry, Uppsala University Hospital, using enzymatic colorimetric assays. The analyses were performed using a Cobas Pro (Roche Diagnostics, Basel, Switzerland) according to standard procedures at the laboratory (CV < 10%).

Verification of a GLP-1 ELISA for canine plasma

A human GLP-1 NL-ELISA assay (Mercodia, Uppsala, Sweden) was verified for canine plasma by evaluating the precision of six canine samples in seven replicates in one run and spike

recovery of one canine plasma sample at two concentration levels. The precision evaluation (at 1.49–6.54 pmol/liter) gave a mean intra-assay CV of 9.3% (range 5.9%–12.7%). Recovery at 75% spiking with low kit control was 103%, while at 50% spiking with medium kit control was 83%. Analysis of GLP-1 in plasma samples from the experiment was performed in duplicate, with mean intra-assay CV of 7.5% (range 5.7%–11.2%), and mean inter-assay CV for low and medium control of 17.0% and 14.8%, respectively. An internal control analyzed in duplicate on the first five runs had mean intra-assay CV of 2.1% and inter-assay CV of 13.5%. Due to an initial low rise in the standard curve, many samples with concentrations in the lower range of the curve had high CV values despite small differences in measured luminescence. Because the rise in the standard curve started to be more pronounced at 2.2 pmol/liter, it was decided to set a lower cutoff at that concentration. Samples for which the two replicates had CV > 12% and mean concentration >2.2 pmol/liter were analyzed a maximum of three times in order to achieve CV < 12%. If that could not be achieved, the concentration was set at the mean of the replicates from all runs ($n = 1$). Samples with mean concentration below 2.2 pmol/liter were given the set concentration of 2.2 pmol/liter, which was considered the detection limit.

Statistical analysis

All statistical analyses were performed in R statistical software version 4.2.1 (R Core Team, 2022). A linear mixed-effects model was fitted with fixed effects of diet, time (categorical), the interaction of diet × time, period and dog group, fasting concentration as a covariate and dog as random effect. As stated previously, there were three dog groups, each following one of the three diet orders. If dog group was not significant, it was removed from the model. In order to detect the time point at which the post-prandial concentration differed from the fasting concentration, a second model in which the fasting value was included as a time point, instead of as a covariate, was also run. The significance levels reported are from the first model, with the fasting value included as a covariate. A model for fasting concentration and area under the curve (AUC) was fitted in the same way, with diet and period as fixed effects as well as dog group (if significant), and dog as random effect. An autoregressive correlation statement was included in all models. The AUC values were approximated using the trapezoid method (AUC function, desctools) for three periods: total postprandial (0–240 min), early postprandial (0–120 min) and late postprandial (120–240 min). Ratio of AUC for insulin to glucose, insulin to GLP-1, and GLP-1 to glucose was calculated and statistically analyzed with the same model as used for the other AUC values. One glucose value for one dog in one period was abnormally low and could not be explained by any physiological reason, so that value was excluded as an analytical error. Variables were natural logarithm-transformed before statistical analysis if they did not meet the prerequisites of homoscedasticity and normality in diagnostic plots (QQ-plot, residual plot and histogram). Significance level was set at $P < 0.05$, while a P-value between 0.05 and 0.1 indicates a tendency. Pairwise comparisons of estimated marginal means were conducted if the main effect was significant and adjustments for multiple comparisons were performed by the Tukey-Kramer method.

Results

All three diets (RYE, WHE, OAT) were well accepted by the dogs, as reported by owners. The BW difference between diet periods was 0.2% ± 3% (mean ± SD) with a maximum difference of 7% increase for one dog in one period. On sampling days, all dogs ate all offered food within the allotted 10 min except for one dog which did not finish all offered food in the first period. The rejected food was weighed and the dog was fed the same caloric amount, as consumed in the first period, on the sampling day of the second period. In the last period, the same dog did not eat any food on the sampling day and was therefore excluded from that period. Moreover, two other dogs were excluded from one diet period each because several attempts to place a peripheral catheter failed and a decision was made to stop further attempts for ethical reasons. Thus, the resulting number of repetitions per diet was: WHE: $n = 16$, OAT: $n = 17$, RYE: $n = 17$.

There was no main effect of diet on the postprandial blood response curves (Figure 1) for any of the variables evaluated and no interaction effect of diet and time. However, the effect of time and fasting concentration as a covariate (time 0) was significant for all variables.

Fasting plasma glucose concentration did not differ between diets (Table 3). When the dogs were fed WHE, the postprandial plasma glucose concentration did not rise significantly from the fasting value (Figure 1A and Supplementary Figure S3). With both the OAT and RYE diets, plasma glucose concentration was significantly elevated from 120 min post feeding. Time to peak value (in our results section defined as the highest numerical value of the curve) was 180 min for both RYE and OAT. Total and late glucose AUC both differed significantly between diets, where OAT resulted in greater AUC glucose concentration than WHE (Table 3).

Fasting plasma insulin concentration was significantly higher for RYE compared with both other diets (Table 3). Postprandial insulin concentration was significantly elevated from 20 min compared with fasting value following WHE and OAT diets, while following RYE the elevation was significant from 40 min (Figure 1B). Insulin concentration showed a numerical peak at 180 min for WHE and OAT, but for RYE the highest numerical value was at the last sampling point (240 min). There was significant overall effect of dog group for the fasting value, but no differences in post-hoc test.

Fasting plasma GLP-1 concentration did not differ between the diets (Table 3). There was no distinct peak for GLP-1 concentration for any of the diets (Figure 1C). The OAT diet resulted in significantly higher GLP-1 AUC than the WHE diet, both when comparing AUC for the whole postprandial phase and for AUC divided in early and late response (Table 3). Moreover, there was a significant overall effect of period on GLP-1 in the total AUC, but no post hoc effect. Likewise, in the late phase of AUC, there was a significant difference between periods, with period 2 being higher than 1. In total, 27.6% of the samples had a GLP-1 concentration at or below the detection limit of 2.2 pmol/liter. The proportion below the detection limit for each diet was: WHE: 33.9%, OAT: 22.7%, RYE: 26.5%.

The ratio of insulin to GLP-1 in the early postprandial phase differed between the diets (Table 3), with a tendency in the post hoc test for highest value for WHE compared with the other diets. There was likewise a tendency for insulin to glucose ratio

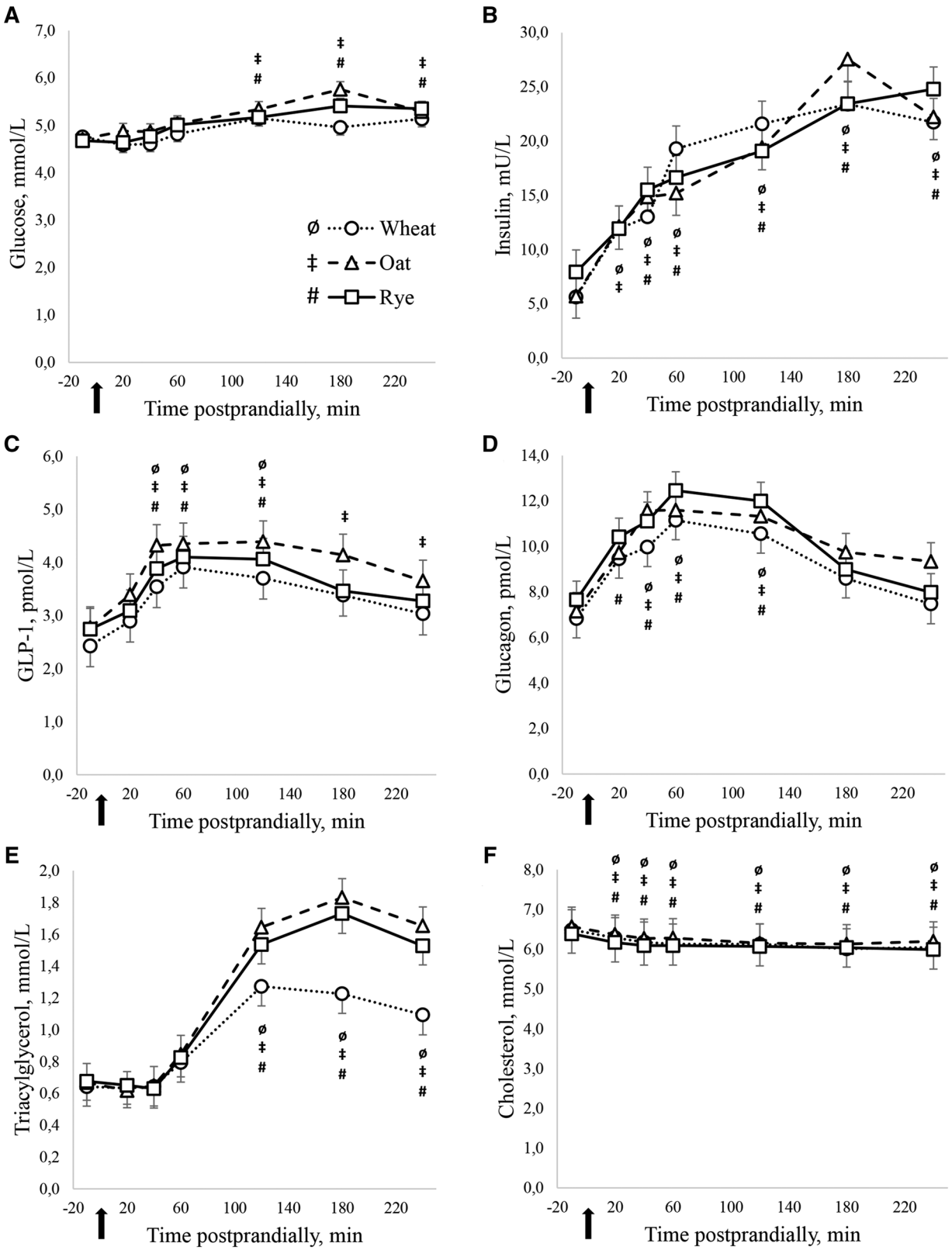

Figure 1. Fasting values and postprandial blood response curves of glucose (A), insulin (B), glucagon like peptide-1 (GLP-1) (C), glucagon (D), triacylglycerol (E), and total cholesterol (F), in dogs fed three different experimental diets (Wheat: $n = 16$, Oat: $n = 17$, Rye: $n = 17$). Shapes and bars indicate estimated marginal means with SE shown in one direction. The arrow indicates time point 0 when dogs were fed each experimental diet. Non-filled shapes indicate a significant time effect, with values differing ($P < 0.05$) from the fasting value. Note that for insulin, the non-filled, significant, shapes for oat and wheat are masked by the non-significant square of rye, at time point 20 min.

Table 3. Blood hormone and metabolite concentrations in dogs fed extruded diets containing whole grains of wheat, oats and rye after a 12 hour fast and for 4 hours postprandially as area under curve (AUC)

	Wheat ± SE (n=16)	Oat ± SE (n=17)	Rye ± SE (n=17)	P-value Diet effect
Fasting concentration				
Glucose, mmol/liter	4.76 ± 0.13	4.71 ± 0.13	4.69 ± 0.13	0.86
Insulin, mU/liter	5.45 ± 0.59[a]	5.88 ± 0.57[a]	7.78 ± 0.57[b]	0.005
GLP-1, pmol/liter	2.45 ± 0.15	2.77 ± 0.15	2.71 ± 0.15	0.13
Glucagon, pmol/liter	6.99 ± 0.55	7.38 ± 0.53	7.5 ± 0.53	0.64
Triacylglycerol, mmol/liter	0.66 ± 0.038	0.68 ± 0.038	0.67 ± 0.038	0.97
Cholesterol, mmol/liter	6.53 ± 0.48	6.65 ± 0.48	6.42 ± 0.48	0.45
AUC total				
Glucose, mmol/liter	1197 ± 33.1[a]	1260 ± 32.4[b]	1236 ± 31.9[a,b]	0.045
Insulin, mU/liter	4614 ± 380	4758 ± 369	4581 ± 361	0.85
GLP-1, pmol/liter	821 ± 93.1[a]	987 ± 92.4[b]	919 ± 92.4[a,b]	0.009
Glucagon, pmol/liter	2273 ± 172	2522 ± 169	2508 ± 169	0.10
Triacylglycerol, mmol/liter	260 ± 24.9[a]	324 ± 24[b]	305 ± 24[a,b]	0.025
Cholesterol, mmol/liter	1469 ± 113	1510 ± 113	1469 ± 113	0.53
Ratio insulin/glucose	3.86 ± 0.28	3.77 ± 0.28	3.66 ± 0.27	0.71
Ratio GLP-1/glucose	0.70 ± 0.070	0.77 ± 0.069	0.75 ± 0.069	0.23
Ratio insulin/GLP-1	6.01 ± 0.56	5.24 ± 0.56	5.47 ± 0.55	0.22
AUC 0–120 min				
Glucose, mmol/liter	583 ± 14.1	601 ± 13.9	593 ± 14	0.21
Insulin, mU/liter	1816 ± 175	1748 ± 172	2145 ± 182	0.27
GLP-1, pmol/liter	429 ± 46.6[a]	491 ± 46.6[b]	474 ± 46.6[a,b]	0.040
Glucagon, pmol/liter	1239 ± 86.4	1297 ± 85.5	1372 ± 85.5	0.064
Triacylglycerol, mmol/liter	104 ± 6.25	116 ± 6.09	111 ± 6.09	0.28
Cholesterol, mmol/liter	745 ± 57.7	764 ± 57.5	742 ± 57.5	0.54
Ratio insulin/glucose	3.51 ± 0.27	3.07 ± 0.27	3.02 ± 0.27	0.082
Ratio GLP-1/glucose	0.74 ± 0.075	0.81 ± 0.075	0.80 ± 0.075	0.16
Ratio insulin/GLP-1	5.09 ± 0.50	4.12 ± 0.50	4.16 ± 0.50	0.042*
AUC 120–240 min				
Glucose, mmol/liter	620 ± 20.8[a]	663 ± 20.1[b]	638 ± 19.8[a,b]	0.049
Insulin, mU/liter	2674 ± 255	2980 ± 241	2737 ± 235	0.51
GLP-1, pmol/liter	398 ± 47.3[a]	495 ± 46.8[b]	447 ± 46.9[a,b]	0.010
Glucagon, pmol/liter	1055 ± 95.9	1225 ± 93.8	1137 ± 93.8	0.075
Triacylglycerol, mmol/liter	156 ± 20.4[a]	209 ± 19.8[b]	193 ± 19.8[a,b]	0.008
Cholesterol, mmol/liter	727 ± 55.6	748 ± 55.2	727 ± 55.2	0.53
Ratio insulin/glucose	4.32 ± 0.37	4.48 ± 0.35	4.24 ± 0.34	0.78
Ratio GLP-1/glucose	0.65 ± 0.073	0.75 ± 0.072	0.71 ± 0.072	0.14
Ratio insulin/GLP-1	7.40 ± 0.77	6.57 ± 0.76	6.91 ± 0.75	0.52

Values are given as estimated marginal means ± SE. Pairwise comparisons of estimated marginal means were conducted if the main effect was significant and then adjusted by the Tukey-Kramer method. Variables that did not meet the prerequisites of homoscedasticity and normality in diagnostic plots were natural logarithm-transformed before statistical analysis.
[a,b]Values within rows with different superscripts differ significantly (P < 0.05)
*Main effect of diet was significant, but post hoc pairwise comparisons adjusted with Tukey-Kramer did not show any significance

to differ between diets in the early postprandial phase, with WHE post hoc having the numerically highest value. There was no effect of diet on the ratio of GLP-1 to glucose, but there was a significant overall effect of period when considering the total postprandial curve and the late response, with period 2 in post hoc tests resulting in numerically highest values.

Fasting serum glucagon concentration did not differ between the diets (Table 3). Glucagon concentration was significantly elevated from 20 min to 120 min following the RYE diet, while following the WHE and OAT diets the elevation was significant between 40 min and 120 min (Figure 1D). Glucagon concentration showed a numerical peak at 60 min for WHE and RYE, while there was no distinct peak for OAT diet. Dog group was significant for the postprandial curve and early AUC phase. Period was significant for both total and early AUC.

Fasting serum concentration of TAG did not differ between the diets (Table 3). The concentration of TAG peaked at 120 min for the WHE diet, while the concentration following the OAT and RYE diets peaked at 180 min (Figure 1E). The OAT diet resulted in higher AUC than WHE, both for total and late AUC (Table 3). Period was significant for the fasting value.

The fasting serum cholesterol concentration did not differ between diets (Table 3). Compared to the fasting value, serum cholesterol concentration was significantly decreased at 20 min and throughout the postprandial period for all diets (Figure 1E).

Glucagon was the only investigated blood variable, for which the postprandial concentration, for all diets, had returned to baseline within the sampling time.

Discussion

This study investigated the effects of including three different whole grain types in complete diets on metabolism and hormonal response in dogs. The main differences observed between

the diets were greater AUC concentrations of plasma glucose, plasma GLP-1 and serum TAG in dogs following OAT compared with WHE, and higher fasting plasma insulin concentration in dogs following RYE compared with both WHE and OAT. Interestingly, the WHE diet tended to result in more insulin per glucose and GLP-1 than the other two diets.

In general, concentrations of the different variables in blood followed a similar pattern for all three diets and were within the ranges reported previously in dogs following consumption of mixed meals (Carciofi et al., 2008; Kempe et al., 2008; Söder et al., 2016). As expected, plasma insulin concentration increased rapidly following the meal for all diets, while plasma glucose concentration was increased compared to baseline at 120 min postprandially for two of the diets. However, for all diets the entire postprandial curve remained within normal blood glucose concentrations (Ettinger et al., 2017). Serum glucagon concentration initially increased rapidly, which was likely attributable to the diets containing mixed ingredients and having a low content of rapidly available glucose (Carr et al., 2010; Radulescu et al., 2010). Glucagon concentration then decreased, likely due to the increased concentrations of blood glucose, insulin and GLP-1, which all suppress glucagon secretion from alpha-cells in the pancreas (Holst, 2007; Frayn, 2010). For serum TAG, a distinct increase was seen between 60 and 120 min and values remained elevated throughout the sampling period for all diets, although differences between diets were found both in total and late AUC.

The higher AUC of plasma glucose for the OAT diet compared with WHE was somewhat unexpected, since OAT had a higher content of soluble fiber than WHE. Soluble fiber in oats is dominated by β-glucan, a viscous fiber reported to have glucose-lowering effects compared with control diets in humans (Biörklund et al., 2005; Hartvigsen et al., 2014) and in pigs (Hooda et al., 2010). However, processing of diet ingredients and the form in which fiber is ingested, as well as the concentration, can all impact the effect of dietary fiber. Unlike in the studies cited, the diets in the present study were all extruded. Extrusion can reduce the molecular weight of β-glucan, thereby reducing the viscosity of the fiber and the glucose-lowering effects (Tosh et al., 2008, 2010). We did not measure the molecular weight of β-glucan or the viscosity of the digesta in the present study, so we do not know whether these properties were affected. There may also be other explanations. For example, in a canine in vitro study, starch in oats was observed to be more easily digestible than starch in wheat grain (Bednar et al., 2001), which could explain the higher glucose AUC seen for the OAT diet in the present study. A somewhat similar pattern of high glucose concentration following a diet with oats has been reported in a previous study on dogs in which a basal corn diet was mixed with autoclaved and ground oat groats or whole wheat (Kempe et al., 2008). The diet with oats was found to have a higher post-prandial maximum glucose concentration than the basal corn diet al.ne, while the diet with wheat did not differ from the basal diet (Kempe et al., 2008). In another study in dogs, a diet supplemented with β-glucans extracted from oats did not have any effect on blood glucose (Ferreira et al., 2018). Thus, the glucose-lowering effect of β-glucan has not been confirmed in dogs.

The postprandial glycemic response was overall low with no clear glucose peak, but rather a slow incline in glucose concentration. This was unexpected, but similar response curves have been shown in earlier published studies following postprandial effects from complete diets in dogs. For example, Söder et al. (2016) did not observe a clear glycemic postprandial response after dogs consuming an energy rich meal (Söder et al., 2016). Moreover, a study from Rankovic et al. (2020), presented postprandial glycemic responses from both simple starch diets and commercial extruded diets, including one diet based on wholegrains. Their study showed that the glucose values increased rapidly after consumption of a diet with a high glycemic index, whereas diets with a low glycemic index showed a slower incline with a peak at 120 min postprandially (Rankovic et al., 2020). Similar results were shown in another study in dogs comparing the metabolic effects from simple and complex carbohydrate sources (Adolphe et al., 2012).

The fasting plasma concentration of insulin was higher following the RYE diet than following the other two diets. Insulin is primarily released in response to an increase in blood glucose. The release is further potentiated by incretins, e.g. GLP-1 (Holst, 2007). We did not detect any differences in fasting glucose or GLP-1 concentration that could explain the difference in fasting insulin. No differences were found in postprandial insulin response between the diets. However, the ratio of insulin to glucose in the early postprandial phase was numerically lower following both RYE and OAT compared with WHE, although there was only a tendency for a statistically significant diet effect. This could indicate that less insulin was needed following the RYE and OAT diets to metabolize glucose, an effect which has been observed previously in pigs on comparing rye to whole grain wheat (Theil et al., 2011). However, the effect of rye in that study was to lower postprandial insulin secretion compared with the whole wheat diet, while the glucose concentration was similar.

The OAT diet led to a higher GLP-1 AUC response compared with WHE. One explanation could be the higher AUC of glucose following OAT compared with WHE, since glucose has been shown to stimulate GLP-1 release (Holst, 2007). The higher concentration of soluble fiber in the OAT diet consumed during this diet period could be another explanation, as short-chain fatty acids (SCFA) are produced during fermentation of soluble fiber. Release of GLP-1 is proposed to be stimulated by binding of SCFA to receptors FFA2 and FFA3 (Chambers et al., 2015; Koh et al., 2016). Results from previous studies on dogs fed diets with highly fermentable fiber are conflicting, with one study reporting an increase in plasma GLP-1 concentrations (Massimino et al., 1998) and another no change in GLP-1 concentrations (Bosch et al., 2009). The diet used in the study by Bosch et al. (2009) contained 1.9% soluble dietary fiber, which is similar to the diets used in our study. Massimino et al. (1998) unfortunately did not report the percentage of soluble fiber. Thus, the extent to which fermentation of soluble fiber in the OAT diet in the present study contributed to the higher plasma GLP-1 content is unclear.

The insulin to GLP-1 AUC ratio in the early postprandial phase was affected by diet, with a post hoc tendency for the WHE diet to result in higher insulin release per GLP-1 than the other two diets. Similarly, there was a tendency toward a lower insulin to glucose ratio following the RYE and OAT diets relative to WHE. The numerically lower insulin to GLP-1 and insulin to glucose AUC ratios observed in dogs fed the RYE and OAT diets, might indicate lower circulating insulin concentrations compared with dogs on the WHE diet during the early postprandial period. In the present study, the postprandial response was monitored for four hours, and insulin

concentrations had not yet returned to fasting concentration at the final sampling point. Future studies with a longer sampling duration would therefore be valuable to further characterize these responses.

Fasting and postprandial plasma GLP-1 concentrations in the present study were somewhat lower than those reported previously for dogs (Massimino et al., 1998; Bosch et al., 2009; Lubbs et al., 2010; Deng et al., 2013). However, in the present study, we used an ELISA kit that had not previously been applied to dog plasma. This is further discussed in the limitations section.

The serum glucagon concentration curve was similar following all diets. The main purpose of glucagon is to increase blood glucose concentration in the case or risk of hypoglycemia (Frayn, 2010). Thus, the strongest signal to increase glucagon release is low blood glucose concentration, while high blood glucose and insulin concentrations suppress glucagon release. However, glucagon is also stimulated by ingestion of amino acids, as in a mixed meal with carbohydrates and protein, as seen in previous studies on dogs (Carciofi et al., 2008; Söder et al., 2016). Thus, the observed glucagon concentration curve following all diets in the present study was expected and their similar appearance reflect the comparable chemical composition of the diets.

Serum TAG concentrations following all diets were within or slightly above the range reported previously for healthy dogs on diets of similar chemical composition in regards to fat, protein and total carbohydrate (Downs et al., 1997; Elliott et al., 2012). Postprandial TAG concentration has been observed to vary with the fat content of the diet (Downs et al., 1997), and since the crude fat content of OAT was slightly higher than that in WHE this could be one explanation for the greater TAG AUC following OAT compared with WHE in the present study. Insulin stimulates uptake of TAG in adipocytes (Frayn, 2010), however, we did not detect any differences in post-prandial plasma insulin concentration between the diets that could explain the differences in TAG concentration. Oat consumption has been shown to result in lower blood cholesterol concentration in humans (Lattimer and Haub, 2010), while supplementation with extracted oat-β-glucans has been observed to have this effect in dogs (Ferreira et al., 2018). However, we did not observe any differences in blood cholesterol for any of the diets in our study.

There are some limitations to the study. The dogs participating were privately-owned and did not live in a controlled laboratory environment. The cross-over design of the study, however, limits the effect of differing living environments for the dogs and mitigates problems with differences between dogs in terms of age or breed. Moreover, the owners were members of the staff and students at an agricultural university and thus should have had a good understanding of the importance of following the instructions when participating in an experimental study. Inevitably some dogs needed a shorter period of medication for various reasons. We cannot exclude the possibility that the treatments with NSAID or corticosteroid ointment could have affected the results. However, we have looked at the raw data and the analytical values for these samples did not stand out. We therefore concluded that these treatments should not have any major effect on the results and thus, the samples have not been excluded. Further, the content of available carbohydrates was not controlled in the balancing of diets and rations for each diet, as the diets were calculated to be equal in caloric amount, and not in carbohydrate content. But the higher non-resistant starch content in WHE, compared to OAT, did not result in higher glucose for the WHE diet. Thus, the differences in starch content between diets did not have substantial effect on blood glucose. Another aspect regarding the starch in diets is that in order to formulate recipes suited for extrusion, the starch sources maize and rice were added. But the chemical analysis showed that even though diet OAT contained marginally more rice than WHE, diet WHE still contained somewhat more starch than OAT. We thus conclude that the added starch sources should not have affected the results.

Another potential limitation is the analysis of GLP-1, which was carried out using an ELISA kit that had not been validated in dogs. However, the kit was verified in our in-house laboratory with satisfactory intra-assay precision and recovery results. The hormone GLP-1 is highly conserved in mammals, which should vouch for high sensitivity of the assay, but the degree of amidation varies (Holst, 2007). The kit used is validated for human plasma, in which the amidated forms of GLP-1 dominate, but the kit does not detect the non-amidated forms of GLP-1. Information regarding the exact target site for the assay is not available, but the fact that the non-amidated form is not detected implies that the binding site is at the amidated amino acid. No information regarding the degree of amidation of dog GLP-1 has been found, but both Bosch et al. (2009) and Massimino et al. (1998) measured the amidated form. In those studies, however, GLP-1 was measured using a radioimmunoassay kit. The kit used in the present study detects total GLP-1, and not only the active hormone. As the half-life of GLP-1 in plasma is only a couple of minutes (Holst, 2007), this total detection of active GLP-1 and its metabolites should enable more accurate results. Thus, the relatively low concentrations in plasma were not expected. The information from the manufacturer of the kit indicated no issues with cross-reactivity and specificity, but this information was for human plasma, thus does not guarantee that the same applies to dog samples. However, the result of low concentration does not suggest that specificity was a major problem. Due to the low rise in the standard curve of the ELISA kit used and the fact that many of the samples had low GLP-1 concentration, it proved challenging to obtain acceptable CV values. Thus, the detection limit was set at 2.2 pmol/liter, at which the rise in the standard curve started to be more pronounced. Approximately one in four samples were at or below the detection limit, which imposes limitations on the statistical analysis. The diagnostic plots for the ANOVA analysis were, however, acceptable.

Conclusions

Dogs fed an extruded diet containing whole grain oats had higher postprandial blood concentrations of glucose, GLP-1 and triacylglycerol than dogs fed a diet with whole grain wheat. The diet containing whole grain rye resulted in higher fasting concentration of insulin than the other two diets, but did not differ from the other diets in any other regard. Altogether, in the present study the postprandial response curves were similar between diets which implies that, in dogs, whole rye or oats may not be more beneficial than whole wheat.

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Author Contributions

Hanna Palmqvist (Conceptualization, Data curation, Formal analysis, Investigation, Project administration, Writing—original draft), Sara Ringmark (Conceptualization, Formal analysis, Investigation, Supervision, Writing—review & editing), Johan Dicksved (Conceptualization, Formal analysis, Funding acquisition, Investigation, Supervision, Writing—review & editing), Torbjörn Lundh (Conceptualization, Formal analysis, Investigation, Supervision, Writing—review & editing), and Katja Höglund (Conceptualization, Data curation, Formal analysis, Investigation, Supervision, Writing—original draft, Writing—review & editing)

Supplementary Data

Supplementary data are available at *Journal of Animal Science* online.

Conflict of interest statement. The authors declare no conflicts of interest.

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