






Effect of lysine restriction on compensatory growth, body composition and nitrogen balance of immunocastrated pigs

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ABSTRACT - This study aimed to evaluate the effects of lysine (Lys) restriction on compensatory growth, body composition, and nitrogen balance of growing-finishing pigs before and after immunocastration. Sixty-four entire male pigs (39.2 ± 6.8 kg) were randomly assigned one of four treatments: Control diet (CON; no restriction) or diets with restriction of Lys level in 14 (Lys-14), 28 (Lys-28) and 42% (Lys-42) of estimated Lys requirements for entire growing pigs (Lys restriction phase, from 0 to 28 d). From 29 to 64 d, all animals received the same diet, formulated to meet the nutritional requirements of entire males (repletion phase 1). Repletion phase 2 (from 65 to 86 d) began immediately after the administration of the second dose of immunocastration. The CON diet and common diets fed from 29 to 64 d and 65 to 86 d were formulated to meet or exceed nutrient requirements. Growth performance and body composition variables reduced linearly ($P \leq 0.05$) as dietary Lys restriction increased, except for the final body lipid which tended to reduce linearly ($P < 0.10$). In the repletion phase 1, no difference was observed for average daily feed intake (ADFI), ADG and G:F (ADG/ADFI) among pigs previously fed CON and Lys-restricted diets regardless of the restriction degree ($P > 0.05$). Final body weight (BW) and final body protein were similar between the groups of pigs previously fed CON or Lys-14 diets ($P > 0.05$). At the end of the repletion phase 2, pigs previously fed CON diet had similar final body protein than pigs previously fed Lys-14 or Lys-28 diets. Regarding the highest Lys restriction evaluated (Lys-42), a total catch-up was evidenced only for the final body weight.

Keywords: amino acid, catch-up, protein deposition, precision feeding, uncastrated male

1. Introduction

Compensatory growth is a complex physiological phenomenon in which pigs previously submitted to a period of nutrient and/or feed intake restriction, exhibit a subsequent accelerated growth rate under adequate nutrition (Menegat et al., 2020). Because lysine (Lys) is the first limiting amino acid (AA) for pigs fed corn-soybean meal-based diets, restricted dietary Lys levels for growing and finishing pigs are commonly associated with lower growth performance (lower average daily gain and feed efficiency; ADG and G:F, respectively; Rao et al., 2021) and greater fat mass deposition (Suárez-Belloch et al., 2015).

However, pigs may present faster growth and a greater protein deposition rate when Lys requirements are re-established (Reynolds and O'Doherty, 2006; Mitchell, 2009), which may compensate for the period of Lys restriction. Additionally, several factors may influence the occurrence and extent of compensatory growth, including the degree of Lys restriction and duration of restriction and re-feeding period (Menegat et al., 2020).

Immunocastration in male pigs consists in the application of two doses of an incomplete analogue of gonadotrophin releasing hormone (GnRH) conjugated to an immunogenic carrier protein (Quiniou et al., 2012). The doses are usually administered four weeks apart, with the last dose given four weeks before slaughter (Zamaratskaia and Rasmussen, 2015). In practical terms, immunocastrated pigs have a greater potential for protein deposition rate and better feed efficiency compared with barrows (Dunshea et al., 2001) since they grow as entire males until receiving the second dose. There are many studies that have evaluated compensatory growth in pigs, but there is a lack of studies with immunocastrated male pigs. We hypothesized that immunocastrated male pigs subjected to a period of dietary Lys restriction would exhibit compensatory growth in the subsequent phases when the Lys supply is re-established. However, the occurrence of compensatory growth depends on the degree of Lys restriction. Therefore, our objective was to evaluate the effect of Lys restriction on compensatory growth, body composition, and nitrogen (N) balance of growing-finishing pigs before and after immunocastration.

2. Material and methods

The study was carried out in the experimental facilities of the Universidade Estadual Paulista (Unesp), Faculdade de Ciências Agrárias e Veterinárias, Jaboticabal, SP, Brazil. All experimental procedures were reviewed and approved by the Ethical Committee for the Care and Use of Experimental Animals at the Faculdade de Ciências Agrárias e Veterinárias of the Universidade Estadual Paulista (protocol no. 14150/19).

2.1. Animals, housing, and experimental design

A total of 64 entire male pigs (Agrocere PIC, Rio Claro, Brazil) with an initial body weight (BW) of 39.2 ± 6.8 kg were used in a trial. The animals were identified and housed in a single 95-m² pen (1.19 m²/animal) with a fully concrete floor. At 126 and 154 days old, all animals were injected subcutaneously with 2.0 mL of a commercial vaccine (Vivax®, Zoetis, Brazil) for immunological castration. In the room, the ambient temperature and relative humidity were controlled using an automated evaporative pad cooling system (Big Dutchman, Araraquara, SP, Brazil) and exhaust fans. The temperature was set at 22 °C and recorded every 30 min using two data loggers (Hobo, Onset Computer Corporation, Bourne, MA, USA) located in the middle of the pen and at half the height of the animal's body. Additionally, the pen was equipped with five automatic feeders (Automatic and Intelligent Precision Feeder [AIPF]; University of Lleida, Lleida, Spain, Pomar et al., 2011) and 10 beat-ball drinkers to allow *ad libitum* access to feed and water, respectively. A transponder (plastic button tag containing passive transponders of radio-frequency identification; Allflex, Joinville, SC, Brazil) was inserted in the right ear of each pig using specific tagger pliers, and the animals were introduced to the electronic feeders. The photoperiod was fixed to 12 h of artificial light (06:00 to 18:00 h).

Details of the feeding station (AIPF) were previously reported by Pomar et al. (2011). Briefly, the AIPF identifies each pig when its head is introduced into the feeder and then delivers feed in response to each animal's request according to the assigned experimental feeds (see the Experimental diets section). In this way, any pig in the pen could access any of the feeders and receive the feed prescribed for that animal. One serving consisted of the amount of feed delivered on each effective serving request (the serving size was 25 g). A time lag (18 s) was imposed to ensure that the pigs consumed each serving before requesting a new one. The pigs tended to leave the feeder empty after each feeding visit, and when there were leftovers, they were smaller than one serving size (20 g), which was insignificant compared with the total feed intake during the day. All feeders were calibrated weekly to convert

the feed volumes into feed weights. The use of exclusive identification codes for each pig allowed the recording of individual feed intake throughout the trial. This feature allowed all animals to be housed in the same pen in a single group and allowed each individual to be an experimental unit.

The pigs remained in the experiment for 109 d, which consisted of a 23-d adaptation period and a subsequent 86-d experimental period. The experimental period was divided into three phases: Lysine restriction phase, from 0 to 28 d; repletion phase 1 (entire male condition), from 29 to 64 d; and repletion phase 2 (immunocastrated male condition), from 65 to 86 d. Regardless of the experimental phase, diets were formulated according to NRC (2012) recommendations. The Lys restriction phase consisted of a qualitative restriction of dietary standardized ileal digestible (SID) Lys levels. At the beginning of this phase, pigs were randomly assigned to receive a Control diet (CON; no restriction) or diets with Lys levels restricted by 14% (Lys-14), 28% (Lys-28) and 42% (Lys-42) relative to the estimated Lys requirements for entire growing pigs. In repletion phase 1, all animals received the same diet, formulated according to the nutritional requirements of the entire male category. Repletion phase 2 began immediately after the administration of the second dose of immunocastration (day 65 of the experimental period), and all animals received a common diet formulated according to the nutritional requirements of immunocastrated males.

2.2. Experimental diets

Experimental diets based on corn and soybean meal (Table 1) were formulated after ingredient analyses of dry matter (DM), net energy (NE), crude protein (CP), and AA composition using near-infrared reflectance spectroscopy (NIRS). The diets were formulated based on SID AA, which was calculated using analyzed AA concentrations in each ingredient and SID coefficients from AMINODat® (2021). Furthermore, diets were formulated to meet or exceed the nutritional requirements for each feeding phase, according to the BW range [from 40 to 60 kg (Lys-restriction phase), from 60 to 90 kg (repletion phase 1) and from 90 to 120 kg (repletion phase 2); NRC (2012)]. The restrictive Lys levels in the first-phase diets were achieved by including the inert ingredient kaolin to replace crystalline Lys in the CON diet. For all diets, the ratio of SID AA to SID Lys met or exceeded NRC (2012) recommendations. The diets were steam pelleted (2.5 mm) and provided *ad libitum* through the feeders.

Table 1 - Centesimal and nutritional composition of experimental diets during lysine restriction and repletion phases 1 and 2¹

	Lysine restriction				Repletion phase 1	Repletion phase 2
	CON	Lys-14	Lys-28	Lys-42		
Ingredient composition (%)						
Corn	80.63	80.63	80.63	80.63	81.48	79.94
Soybean meal	13.87	13.87	13.87	13.87	13.35	15.79
Dicalcium phosphate	1.28	1.28	1.28	1.28	1.23	1.10
Limestone	0.54	0.54	0.54	0.54	0.55	0.53
Sodium chloride	0.23	0.23	0.23	0.23	0.23	0.23
Kaolin	1.69	1.92	2.15	2.38	1.50	0.95
Biolys, 54.6 (%)	0.69	0.46	0.23	0.00	0.67	0.38
DL-Methionine	0.09	0.09	0.09	0.09	0.08	0.01
L-Threonine	0.12	0.12	0.12	0.12	0.11	0.03
L-Tryptophan	0.03	0.03	0.03	0.03	0.03	-
L-Valine	0.01	0.01	0.01	0.01	0.01	-
Choline chloride	0.06	0.06	0.06	0.06	0.06	0.06
Mineral premix ²	0.10	0.10	0.10	0.10	0.10	0.10
Vitamin premix ³	0.40	0.40	0.40	0.40	0.40	0.30
Maltodextrin	-	-	-	-	-	0.50
Soy oil	0.25	0.25	0.25	0.25	0.20	0.10

Continues...

Table 1 (Continued)

	Lysine restriction				Repletion phase 1	Repletion phase 2
	CON	Lys-14	Lys-28	Lys-42		
Calculated chemical composition⁴						
Metabolizable energy (kcal/kg)	3,366	3,357	3,348	3,339	3,372	3,388
Net energy (kcal/kg)	2,593	2,586	2,579	2,573	2,600	2,600
Crude fiber (%)	2.64	2.64	2.64	2.64	2.64	2.72
Crude protein (%)	14.44	14.26	14.08	13.90	14.25	14.87
SID lysine (%)	0.89	0.77	0.64	0.52	0.87	0.77
SID methionine (%)	0.30	0.30	0.30	0.30	-	-
SID methionine + cysteine (%)	0.50	0.50	0.50	0.50	0.49	0.44
SID threonine (%)	0.54	0.54	0.54	0.54	0.53	0.48
SID tryptophan (%)	0.15	0.15	0.15	0.15	0.15	0.13
SID isoleucine (%)	0.48	0.48	0.48	0.48	0.47	0.51
SID leucine (%)	1.20	1.20	1.20	1.20	1.19	1.26
SID valine (%)	0.58	0.58	0.58	0.58	0.57	0.60
SID arginine (%)	0.75	0.75	0.75	0.75	0.74	0.81
SID phenylalanine (%)	0.60	0.60	0.60	0.60	-	-
SID histidine (%)	0.34	0.34	0.34	0.34	0.33	0.36
Calcium (%)	0.66	0.66	0.66	0.66	0.65	0.60
STTD phosphorus (%)	0.31	0.31	0.31	0.31	0.30	0.28
Sodium (%)	0.11	0.11	0.11	0.11	0.11	0.11
Chloride (%)	0.22	0.22	0.22	0.22	0.22	0.22
Analyzed chemical composition⁵						
Dry matter (%)	88.50	88.85	88.60	88.99	88.55	88.48
Metabolizable energy (kcal/kg)	3,222	3,264	3,238	3,219	3,228	3,213
Net energy (kcal/kg)	2,467	2,507	2,484	2,468	2,469	2,433
Crude fiber (%)	2.90	2.60	2.60	2.80	2.60	2.50
Crude protein (%)	14.54	13.87	14.30	14.04	14.20	14.87
SID lysine (%)	1.01	0.84	0.75	0.61	1.04	0.84
SID methionine (%)	0.32	0.31	0.32	0.30	-	-
SID methionine + cysteine (%)	0.57	0.56	0.57	0.56	0.58	0.52
SID threonine (%)	0.61	0.59	0.61	0.59	0.63	0.56
SID isoleucine (%)	0.54	0.53	0.54	0.53	0.56	0.61
SID leucine (%)	1.25	1.27	1.27	1.28	1.27	1.46
SID valine (%)	0.67	0.66	0.66	0.65	0.69	0.72
SID arginine (%)	0.86	0.82	0.84	0.82	0.89	0.88
SID phenylalanine (%)	0.66	0.65	0.66	0.65	-	-
SID histidine (%)	0.38	0.38	0.38	0.37	0.39	0.40

SID - standardized ileal digestible; STTD - standardized total tract digestible.

¹ CON (Control), Lys-14, Lys-28, and Lys-42 represent 100, 86, 72, and 58% of lysine requirements, respectively (NRC, 2012). Pigs' category: Entire male condition in the lysine restriction phase (from 0 to 28 days) and repletion phase 1 (from 29 to 64 days). Immunocastrated condition in repletion phase 2 (from 65 to 86 days).

² Mineral premix supplied (per kg of diet): Manganese (40 mg); copper (15 mg); iron (24.93 mg); cobalt (0.168 mg); iodine (1.416 mg); and zinc (74.971 mg).

³ Vitamin premix supplied (per kg of diet): Folic acid (0.504 mg); D-pantothenic acid (12 mg); biotin (0.144 mg); niacin (21 mg); selenium (0.2516 mg); vit. A (4,400 IU); vit. B1 (1.8 mg); vit. B12 (21.6 mcg); vit. B2 (4.68 mg); vit. B6 (2.52 mg); vit. D3 (1,400 IU); vit. E (20 IU); and vit. K3 (2.16 mg).

⁴ Nutrient content of diets based on estimated nutrient contents of ingredients, according to AMINODat® 6.0 (2021).

⁵ Amino acids content of diets were analyzed using the high-performance liquid chromatography (HPLC). Crude protein (Nitrogen analyzer for Dumas method - Vario MAX cube, Elementar), dry matter (Thermo gravimetric analyzer; TGA 701, LECO), crude fiber, metabolizable and net energy values.

2.3. Analytical procedures

Representative samples (200 g) of feed were taken once weekly during the experimental period and pooled per experimental treatment and phase. Each sample was subjected to analysis using high-performance liquid chromatography (HPLC) at the AMINOLab of Evonik Operations GmbH (Hanau, Germany) to estimate total AA content (AA analyzer – 30 series, Biochrom), CP (nitrogen analyzer using the Dumas method – Vario MAX cube, Elementar), DM (thermogravimetric analyzer – TGA 701, LECO), ether extract, ash, crude fiber, and metabolizable and net energy contents.

2.4. Growth performance and body composition measurements

Animals were weighed individually without fasting at the beginning and end of each experimental phase (days 0, 28, 64, and 86). Feed intake was calculated using the feeding information of each pig (AIPF software). Growth performance was evaluated based on final BW, average daily feed intake (ADFI; kg/d), ADG (kg/d), G:F, and NE intake (MJ/d).

Total body lean and fat mass were measured at the beginning and end of each experimental phase by dual-energy X-ray absorptiometry (DXA; GE 205 Lunar Prodigy Advance; GE Healthcare, Madison, WI, USA). For this procedure, animals were fasted for 8 h before being sedated by intramuscular injection of xylazine (1.5 mg/kg) and ketamine (10–15 mg/kg). Pigs were scanned in the prone position using the total body scanning mode in the manufacturer-provided software (Lunar enCORE software, version 8.10.027; GE Healthcare). After completing post-anesthetic recovery, the animals were returned to the pen.

2.5. Calculations and statistical analysis

The DXA body lean and fat masses were converted to total body protein and body lipid according to Pomar and Rivest (1996). Protein and lipid deposition (PD and LD, respectively; g/day) were calculated as the difference between the respective body constituents estimated from the DXA readings at the beginning and end of each experimental phase (from 0 to 28 days, from 29 to 64 days, and from 65 to 86 days). The energy retained (MJ/d) was calculated assuming that protein gain contained 23.8 MJ/kg (Kleiber, 1961) and fat contained 39.581 MJ/kg (Sainz and Wolff, 1988). NE intake (MJ/d) was measured based on individual feed intake and the analyzed NE content of the experimental diets. Nitrogen excretion (g/d) was obtained for each scanned pig by subtracting the N retention (protein deposition divided by 6.25) from the N intake (estimated as [CP in the diet multiplied by the ADFI] divided by 6.25). Nitrogen efficiency (%) was calculated by dividing the N retention by the N intake.

The Box-Cox and Cramér-von Mises tests were used to verify the homogeneity of variances and normality of the studentized residuals, respectively. For analysis of variance, data were analyzed per experimental phase using the GLIMMIX procedure (SAS, version 9.4; SAS Inst. Inc., Cary, NC) according to the following model:

$$Y_{ij} = \mu + \tau_i + e_{ij}, \quad (1)$$

in which Y_{ij} represents the dependent variable in each phase receiving Lys level i on experimental unit j ; μ = the overall mean; τ_i = fixed effect of dietary Lys level; and e_{ij} = random error corresponding to each observation.

In all experimental phases, dietary Lys levels in the first phase (Lys-restriction phase) were considered fixed effects. The individual pig was considered the experimental unit. For each phase, when there were differences among dietary Lys levels ($P \leq 0.05$), adjusted means were compared using the Tukey–Kramer *post hoc* test. Orthogonal polynomial contrasts were applied to test the linear and quadratic responses according to increased dietary Lys level variation. The significance level adopted for all analysis was 5% ($P \leq 0.05$), and a trend towards significance was considered if $0.05 < P \leq 0.10$.

3. Results

3.1. General observations

The average room ambient temperature was 21.1 ± 2.0 °C and the daily relative humidity averaged 70%. These values indicate that animals were maintained under thermoneutral conditions. No pigs were removed from the trial, and no health issues were detected during the experimental period.

3.2. Lysine restriction phase – Entire male pigs condition

Regarding performance traits, pigs fed the CON diet had similar final BW to pigs fed the Lys-14 diet ($P>0.05$) and greater final BW than those fed the Lys-28 or Lys-42 diets ($P\leq 0.05$; Table 2). There was no difference in final BW among pigs fed the Lys-restricted diets ($P>0.05$). Greater ADG and G:F were observed in pigs fed the CON diet compared with pigs fed the Lys-restricted diets ($P\leq 0.05$). Among Lys-restricted diets, pigs fed the Lys-14 diet had similar ADG and G:F to pigs fed the Lys-28 diet ($P>0.05$), greater ADG and G:F than pigs that received the Lys-42 diet ($P\leq 0.05$). Similar ADG ($P>0.05$) and greater G:F ($P\leq 0.05$) were observed in pigs fed the Lys-28 diet compared with those fed the Lys-42 diet.

Table 2 - Performance, body composition and N balance of entire male pigs during lysine restriction phase¹

Item ²	Treatment				SEM ³	P-value ⁴		
	CON	Lys-14	Lys-28	Lys-42		Anova	Lin ⁵	Quad ⁵
Number of animals	16	16	16	16				
Initial conditions (day 0)								
Initial BW (kg)	36.73	37.04	36.15	36.83	1.57	0.98	0.92	0.87
Initial body lipid ⁶ (kg)	7.94	8.02	7.93	8.01	0.25	0.98	0.86	0.88
Initial body protein ⁶ (kg)	5.01	5.02	4.95	5.02	0.27	0.96	0.84	0.85
Performance (from 0 to 28 days)								
Final BW (kg)	62.84a	58.65ab	55.02b	52.81b	2.49	0.03	0.00	0.68
ADG (kg)	0.93a	0.77b	0.67bc	0.57c	0.04	<0.01	<0.01	0.50
ADFI (kg)	1.97	1.84	1.76	1.70	0.09	0.15	0.02	0.69
G:F	0.47a	0.41b	0.39b	0.34c	0.01	<0.01	<0.01	0.75
NE intake (MJ/d)	20.37	19.20	18.18	17.35	0.91	0.11	0.02	0.85
Body composition (from 0 to 28 days)								
Final body lipid ⁶ (kg)	13.06	12.34	12.32	11.77	0.51	0.37	0.10	0.87
Final body protein ⁶ (kg)	9.26a	8.52ab	7.85bc	7.43c	0.40	0.01	0.00	0.67
Lipid deposition (LD; g/d)	184a	152b	157ab	134b	11.58	0.03	0.01	0.71
Protein deposition (PD; g/d)	151a	125b	105c	87c	6.40	<0.01	<0.01	0.51
LD/PD	1.22b	1.19b	1.50a	1.53a	0.05	<0.01	<0.01	0.62
Energy retained (MJ/d)	10.79a	8.93b	8.66b	7.33b	0.59	0.00	<0.01	0.65
NE intake:Energy retained	1.91c	2.29ab	2.12bc	2.44a	0.10	0.01	0.00	0.77
Nitrogen (N) balance (from 0 to 28 days)								
N retained (g/d)	24.08a	19.99b	16.72c	13.94c	1.02	<0.01	<0.01	0.51
N intake (g/d)	45.91a	40.62ab	40.02b	37.73b	1.99	0.04	0.01	0.44
N efficiency (%)	52.48a	48.93a	42.28b	36.82c	1.30	<0.01	<0.01	0.45

¹ CON (Control), Lys-14, Lys-28, and Lys-42 represent 100, 86, 72, and 58% of lysine requirements, respectively (NRC, 2012).

² BW: body weight, ADG: average daily gain, ADFI: average feed intake, G:F: ADG/ADFI, and energy retained: energy retained as protein and fat considering that protein gain contained 23.8 MJ/kg (Kleiber, 1961) and fat contained 39.581 MJ/kg (Sainz and Wolff, 1988).

³ Standard error of the mean.

⁴ Probability values considering the effect of dietary treatments (Anova). a,b,c - Within a row, means with different letters are affected by treatments according to Tukey's test ($P<0.05$).

⁵ Orthogonal polynomial contrast analysis was used to determine the linear (Lin) and quadratic (Quad) responses according to increased dietary Lys level variation.

⁶ Body protein and lipid levels were estimated according to Pomar and Rivest (1996) from dual-energy X-ray absorptiometry measurements (DXA).

For body composition, pigs fed the CON diet had similar final body protein content to pigs fed the Lys-14 diet ($P>0.05$) and greater final body protein content than those fed the Lys-28 or Lys-42 diets ($P\leq 0.05$). Among Lys-restricted diets, pigs fed the Lys-14 diet had similar final body protein content to pigs fed the Lys-28 diet ($P>0.05$) and greater values than those fed the Lys-42 diet ($P\leq 0.05$); whereas final body protein content did not differ between pigs that received the Lys-28 or Lys-42 diets ($P>0.05$). In general, higher LD and PD but a lower LD:PD ratio were observed in pigs fed the CON diet compared with those fed the Lys-restricted diets ($P\leq 0.05$). Exceptions were observed between CON and Lys-28 for LD and between CON and Lys-14 for LD/PD, whose values were similar ($P>0.05$). There was no difference in LD among pigs fed Lys-restricted diets ($P>0.05$). However, greater PD and lower LD/PD were observed in pigs fed Lys-14 diet than in pigs fed Lys-28 or Lys-42 diets ($P\leq 0.05$), whereas both variables were similar between pigs that received the Lys-28 or Lys-42 diets ($P>0.05$). Pigs fed the CON diet had greater energy retained than those fed the Lys-restricted diets ($P\leq 0.05$), and no difference was observed among pigs that received the Lys-restricted diets ($P>0.05$). Lower NE intake:energy retained was observed in pigs fed the CON diet compared with those fed the Lys-14 or Lys-42 diets ($P\leq 0.05$), whereas NE intake:energy retained was similar between pigs fed the CON or Lys-28 diets ($P>0.05$). Among Lys-restricted diets, pigs fed the Lys-14 diet had similar NE intake:energy retained to pigs fed the Lys-28 or Lys-42 diets ($P>0.05$), and lower NE intake:energy retained was observed in pigs fed the Lys-28 diet compared with pigs fed the Lys-42 diet ($P\leq 0.05$).

Regarding N balance, pigs fed the CON diet had greater N retained ($P\leq 0.05$) and similar N intake and N efficiency compared with pigs fed the Lys-14 diet ($P>0.05$), whereas N retained, N intake, and N efficiency were greater in pigs fed the CON diet than in those fed the Lys-28 or Lys-42 diets ($P\leq 0.05$). There was no difference in N intake among pigs fed the Lys-restricted diets ($P>0.05$). However, pigs fed the Lys-14 diet had greater N retained and N efficiency than pigs that received the Lys-28 or Lys-42 diets ($P\leq 0.05$), whereas pigs fed the Lys-28 diet had similar N retained ($P>0.05$) and greater N efficiency ($P\leq 0.05$) than pigs fed the Lys-42 diet.

There was a linear effect ($P\leq 0.05$) on growth performance, body composition, and N balance variables. All variables decreased (or tended to decrease) linearly as dietary Lys restriction increased. No quadratic effect was observed for any of the variables studied ($P>0.05$).

3.3. Repletion phase 1 – Entire male pigs phase

In repletion phase 1, when all animals received a common diet (formulated according to the nutritional requirements of entire males), different levels of dietary Lys restriction during the previous phase did not affect ADFI, ADG, G:F, or NE intake ($P>0.05$; Table 3). Final BW was similar to pigs that received the CON and Lys-14 diets during the Lys-restriction phase ($P>0.05$) and tended to be greater in pigs previously fed the CON diet than in those previously fed the Lys-28 or Lys-42 diets ($P<0.10$). There was no difference in the final BW among pigs fed the Lys-restricted growing diets ($P>0.05$).

Regarding body composition, there were no differences in final body lipid, final body protein, LD, LD/PD, and energy retained among pigs fed the Lys-restricted growing diets ($P>0.05$). Greater final body lipid and LD were observed in pigs previously fed the CON diet than in those previously fed the Lys-restricted diets ($P\leq 0.05$). Final body protein and energy retained were similar between pigs fed the CON and Lys-14 diets during the Lys-restriction phase ($P>0.05$), whereas both variables tended to be greater in pigs previously fed the CON diet than in those previously fed the Lys-28 or Lys-42 diets ($P<0.10$). Pigs fed the CON diet during the Lys-restriction phase tended to have greater LD/PD than pigs previously fed the Lys-14 or Lys-42 diets ($P<0.10$) and similar LD/PD to pigs previously fed the Lys-28 diet.

In repletion phase 1, no difference in N balance was found among the experimental treatments applied during the previous phase ($P>0.05$). For growth performance, body composition, and N balance variables, there were linear effects ($P\leq 0.05$) on final BW, final body lipid, final body protein, LD, LD/PD, energy retained, and N efficiency; and a tendency for linear effects on ADFI, NE intake, NE

intake:energy retained, and N retained ($P<0.10$). All variables reduced (or tended to reduce) linearly as dietary Lys restriction was intensified during the Lys-restriction phase. No quadratic effect was observed for any of the variables studied ($P>0.05$).

Table 3 - Influence of lysine restriction phase during repletion phase 1¹

Item ²	Treatment				SEM ³	P-value ⁴		
	CON	Lys-14	Lys-28	Lys-42		Anova	Lin ⁵	Quad ⁵
Number of animals	16	16	16	16				
Performance (from 29 to 64 days)								
Final BW (kg)	101.81x	94.46xy	90.72y	88.99y	3.58	0.06	0.01	0.42
ADFI (kg)	2.60	2.39	2.33	2.34	0.10	0.22	0.07	0.27
ADG (kg)	1.11	1.05	1.02	1.03	0.04	0.33	0.11	0.34
G:F	0.43	0.44	0.44	0.44	0.01	0.77	0.32	0.77
NE intake (MJ/d)	26.88	24.75	24.08	24.23	1.06	0.22	0.07	0.27
Body composition (from 29 to 64 days)								
Final body lipid ⁶ (kg)	17.34x	15.04y	15.01y	14.26y	1.16	0.06	0.01	0.33
Final body protein ⁶ (kg)	16.98x	15.94xy	15.14y	14.97y	0.62	0.10	0.02	0.47
Lipid deposition (LD; g/d)	123a	80b	84b	72b	13.06	0.03	0.01	0.21
Protein deposition (PD; g/d)	221	217	210	215	7.56	0.75	0.46	0.53
LD/PD	0.54x	0.37y	0.40xy	0.34y	0.05	0.05	0.02	0.31
Energy retained (MJ/d)	10.11x	8.37xy	8.01y	7.97y	0.63	0.06	0.02	0.17
NE intake:Energy retained	2.75	3.16	3.13	3.16	0.14	0.13	0.06	0.19
Nitrogen (N) balance (from 29 to 64 days)								
N retained (g/d)	59.08	54.38	52.93	53.26	2.33	0.22	0.07	0.27
N intake (g/d)	35.39	34.75	33.59	34.43	1.21	0.75	0.46	0.53
N efficiency (%)	60.44	63.56	63.88	65.04	1.36	0.11	0.02	0.47

¹ In the lysine restriction phase, the treatments were CON (Control), Lys-14, Lys-28, and Lys-42 which represent 100, 86, 72, and 58% of lysine requirements, respectively (NRC, 2012). In the repletion phase 1, all pigs were fed the same diet.

² BW: body weight, ADG: average daily gain, ADFI: average feed intake, G:F: ADG/ADFI, and energy retained: energy retained as protein and fat considering that protein gain contained 23.8 MJ/kg (Kleiber, 1961) and fat contained 39.581 MJ/kg (Sainz and Wolff, 1988).

³ Standard error of the mean.

⁴ Probability values considering the effect of dietary treatments (Anova). a,b,c - Within a row, means with different letters are affected by treatments according to Tukey's test ($P<0.05$). x,y - Within a row, means with different letters are a tendency according to Tukey's test ($0.05 < P < 0.10$).

⁵ Orthogonal polynomial contrast analysis was used to determine the linear (Lin) and quadratic (Quad) responses according to increased dietary Lys level variation.

⁶ Body protein and lipid levels were estimated according to Pomar and Rivest (1996) from dual-energy X-ray absorptiometry measurements (DXA).

3.4. Repletion phase 2 – Immunocastrated male pigs phase

In repletion phase 2, when a common diet was provided (formulated according to the nutritional requirements of immunocastrated males), growth performance variables were not affected by the experimental diets applied during the restriction phase ($P>0.05$; Table 4). Pigs previously fed the CON diet had similar final body protein content to pigs previously fed the Lys-14 or Lys-28 diets and tended to have greater final body protein content than those previously fed the Lys-42 diet ($P<0.10$). There was no difference in the final body protein content among pigs fed the Lys-restricted growing diets ($P>0.05$). The pattern of change in final BW throughout the experimental phases is shown in Figure 1.

For growth performance and body composition variables, there was a linear effect for final body protein ($P\leq 0.05$) and a tendency for a linear effect on final BW ($P<0.10$). Both variables decreased (or tended to decrease) linearly as dietary Lys restriction increased during the Lys-restriction phase. No quadratic effect was observed for any of the variables studied ($P>0.05$).

Table 4 - Influence of lysine restriction phase during repletion phase 2¹

Item ²	Treatment				SEM ³	P-value ⁴		
	CON	Lys-14	Lys-28	Lys-42		Anova	Lin ⁵	Quad ⁵
Number of animals	16	16	16	16				
Performance (from 65 to 86 days)								
Final BW (kg)	133.39	127.80	123.21	122.37	4.45	0.28	0.06	0.59
ADFI (kg)	3.67	3.40	3.30	3.40	0.16	0.40	0.21	0.23
ADG (kg)	1.54	1.48	1.46	1.52	0.05	0.71	0.70	0.27
G:F	0.42	0.44	0.45	0.44	0.01	0.33	0.11	0.31
NE intake (MJ/d)	37.42	34.68	33.60	34.70	1.67	0.40	0.21	0.23
Body composition (from 65 to 86 days)								
Final body lipid ⁶ (kg)	20.34	18.68	19.14	17.57	1.20	0.39	0.13	0.97
Final body protein ⁶ (kg)	19.67x	19.00xy	18.21xy	17.36y	0.69	0.08	0.01	0.88
Lipid deposition (LD; g/d)	261	264	275	274	35.65	0.99	0.75	0.95
Protein deposition (PD; g/d)	228	214	205	207	10.40	0.37	0.11	0.40
LD/PD	1.29	1.23	1.43	1.39	0.22	0.89	0.60	0.94
Energy retained (MJ/d)	15.68	15.46	15.68	16.06	1.36	0.99	0.82	0.81
NE intake:Energy retained	2.52	2.37	2.19	2.28	0.17	0.49	0.20	0.45
Nitrogen (N) balance (from 65 to 86 days)								
N retained (g/d)	80.81	73.07	71.72	75.01	3.86	0.34	0.27	0.14
N intake (g/d)	36.46	34.20	34.00	33.13	1.50	0.43	0.12	0.62
N efficiency (%)	47.81	48.29	48.74	45.21	2.95	0.80	0.56	0.47

¹ In the lysine restriction phase, the treatments were CON (Control), Lys-14, Lys-28, and Lys-42 which represent 100, 86, 72, and 58% of lysine requirements, respectively (NRC, 2012). In the repletion phase 2, all pigs (immunocastrated condition) received the same diet.

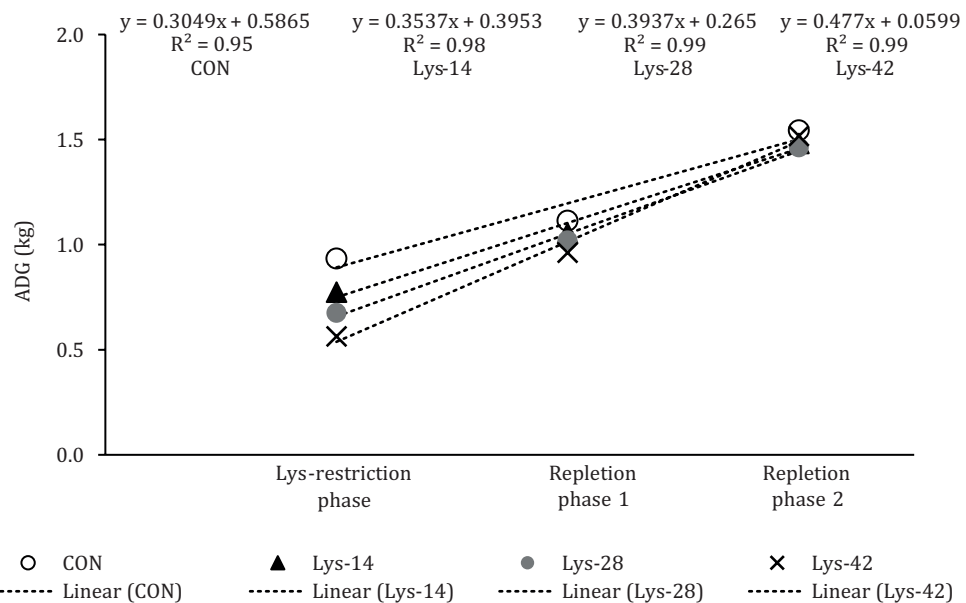
² BW: body weight, ADG: average daily gain, ADFI: average feed intake, G:F: ADG/ADFI, and energy retained: energy retained as protein and fat considering that protein gain contained 23.8 MJ/kg (Kleiber, 1961) and fat contained 39.581 MJ/kg (Sainz and Wolff, 1988).

³ Standard error of the mean.

⁴ Probability values considering the effect of dietary treatments (Anova). x,y - Within a row, means with different letters are a tendency according to Tukey's test (0.05 < P < 0.10).

⁵ Orthogonal polynomial contrast analysis was used to determine the linear (Lin) and quadratic (Quad) responses according to increased dietary Lys level variation.

⁶ Body protein and lipid levels were estimated according to Pomar and Rivest (1996) from dual-energy X-ray absorptiometry measurements (DXA).



¹ Entire male condition in the Lys-restriction phase (from 0 to 28 days) and repletion phase 1 (from 29 to 64 days). Immunocastrated condition in repletion phase 2 (from 65 to 86 days).

² In the Lys-restriction phase, the treatments were CON (Control), Lys-14, Lys-28, and Lys-42 which represent 100, 86, 72, and 58% of Lys requirements, respectively (NRC, 2012). In the repletion phases 1 and 2, all pigs received a common diet (formulated according to the nutrition requirements of each category; NRC, 2012).

Figure 1 - Linear equations of average daily gain (ADG) of pigs¹ through experimental phases².

4. Discussion

Our main objective was to evaluate the effect of Lys restriction on compensatory growth, body composition, and N balance of growing–finishing pigs before and after immunocastration. For compensatory growth to occur, initial growth performance must be limited (O’Connell et al., 2006). The NRC (2012) SID Lys recommendation is 0.89% for 50- to 75-kg entire male pigs with a daily protein deposition of 150 g. Therefore, the different dietary levels of SID Lys restriction used in this experiment (0.77, 0.64, and 0.52% for Lys-14, Lys-28, and Lys-42, respectively) were chosen to create a reduction in growth performance with a negative impact on body composition, which could induce subsequent compensatory growth. We demonstrated that immunocastrated male pigs previously subjected to early dietary Lys restriction may compensate for their reduced growth performance. However, since the duration of the Lys-restriction phase was similar for all pigs, this effect was influenced mainly by the severity of Lys restriction. In addition, our major and novel finding is that pigs fed a diet with 42% Lys restriction were able to exhibit compensatory growth, but complete compensatory growth was observed only for final BW.

In the current study, although treatments did not differ for ADFI, pigs fed the CON diet had greater growth performance (final BW, ADG, and G:F) and protein deposition compared with Lys-restricted pigs, regardless of the degree of restriction. Similarly, a Lys-restricted diet for finishing pigs resulted in lower ADG and G:F (without effect on ADFI; Rao et al., 2021) and lower loin weight (Suárez-Belloch et al., 2015) compared with nonrestricted pigs. However, the magnitude of the impact on growth performance and body composition observed in our study was dependent on the degree of Lys restriction. For instance, growth performance, body composition, and N balance variables decreased (or tended to decrease) linearly as dietary Lys restriction increased. In agreement, linear growth reduction (lower ADG and greater feed conversion ratio) with more severe Lys restrictions (6.3, 5.6, 4.2, and 3.2 g/kg SID Lys) was also observed for finishing pigs (Suárez-Belloch et al., 2015). Still, Remus et al. (2020) observed that ADG, G:F, and protein deposition decreased linearly when dietary Lys restriction for growing–finishing pigs increased (pigs fed 60, 70, 80, 90, and 100% of Lys in relation to their individual daily requirements).

The underlying mechanisms of Lys-restriction on performance and body composition include a complex metabolic process. A period of Lys restriction promotes metabolic and endocrine changes in energy partitioning toward lipid deposition rather than protein deposition (Menegat et al., 2020). Lower plasma concentrations of insulin-like growth factor-1 (IGF-1; Ishida et al., 2012) and glucocorticoids (cortisol and corticosterone) associated with greater concentrations of leptin (Martínez-Ramírez et al., 2009) were observed in pigs fed low-Lys diets compared with nonrestricted pigs. IGF-1 is a major regulator of anabolic status and protein synthesis in skeletal muscle (Yoshida and Delafontaine, 2020) and glucocorticoids stimulate the muscle protein degradation (Kuo et al., 2013). Leptin, in turn, is a regulatory hormone of lipid deposition (Picó et al., 2022).

Therefore, results of lower LD/PD observed in the current study for pigs fed CON and Lys-14 diets than those fed Lys-28 and Lys-42 diets, suggest that only pigs fed Lys-14 diet had an energetic metabolic pattern similar to nonrestricted pigs, indicating a less pronounced effect of restriction in these animals. Accordingly, the efficiency of N retention (N retained/N intake) was greater for pigs fed CON and Lys-14 diets compared with those fed more restricted diets (that is, Lys-28 and Lys-42). During the restriction period, pigs fed CON diet had greater energy retained and lower NE intake:energy retained compared to those fed Lys restricted diets (an exception was observed for NE intake:energy retained in the comparison between CON and Lys-28). Since there was no difference in NE intake among all treatments, the greater protein and lipid deposition observed for pigs fed CON diet compared with restricted pigs may explain the greater energy retained and, consequently, lower NE intake:energy retained.

The restricted diets were not formulated according to the ideal protein model, resulting in unbalanced Lys:AA ratios. Some AAs other than Lys may have been supplied in excess relative to requirements,

being catabolized in the liver through transamination or oxidative deamination, with the amino group entering the urea cycle for excretion of surplus nitrogen (Wang et al., 2018). This may explain the lower nitrogen retention observed in the more restrictive treatments.

Furthermore, any excess carbon skeletons from deaminated AAs may have contributed to lipogenesis (Liao et al., 2015) in the more restricted treatments. We hypothesized that since the 28% Lys restriction group did not differ from the control in lipid deposition, the AA imbalance may have affected lipogenesis only at higher levels of Lys restriction. Additionally, lower energy retention in the restricted diets could partly result from the increased caloric cost of AA catabolism, due to the energetic cost of AA deamination. Therefore, this AA imbalance may have impacted the compensatory growth response in the following phases, even though the effects observed after the restriction period may not be exclusively attributable to Lys restriction.

After the respective nutrient restriction period, pigs were fed a Lys-unrestricted diet in order to evaluate the occurrence of a compensatory growth response. In repletion phase 1, no differences were observed for ADFI, ADG, and G:F between pigs previously fed the CON and Lys-restricted diets, regardless of the degree of restriction. In pigs, compensatory growth can occur through an increased growth rate due to increased feed intake and/or improved feed efficiency (Menegat et al., 2020). Since treatments did not differ for ADFI in both phases (Lys-restriction and repletion phase 1), it can be suggested that the compensatory growth response observed in repletion phase 1 was mainly driven by an improvement in G:F, allowing previously Lys-restricted pigs to reach similar G:F values to pigs previously fed the CON diet. These findings are consistent with those reviewed by Menegat et al. (2020), who reported that, in the case of Lys restriction, compensatory growth in pigs is driven by improvements in G:F rather than by an increase in ADFI.

Pigs may present complete or incomplete compensatory growth, which refers to the occurrence of a faster growth rate that leads to similar (complete) or lower (incomplete) BW compared with nonrestricted pigs at a similar age (Skiba, 2005). In repletion phase 1, final BW and final body protein content were similar between pigs fed the CON and Lys-14 diets during the Lys-restriction phase. These results suggest that pigs previously fed the Lys-14 diet (86% of Lys requirements; NRC, 2012) were able to recover final BW and protein deposition, confirming the occurrence of complete compensatory growth in these animals.

The degree of Lys restriction is indeed one of the factors that affect the ability of pigs to compensate for their performance and body composition. For instance, Yang et al. (2009) observed that pigs fed diets with 20% and 30% lower dietary Lys levels compared with CON diets exhibited compensatory growth, whereas a 40% reduction did not induce a compensatory response. Therefore, the severity of dietary Lys reduction should be considered when applying the concept of compensatory growth as a potential strategy to improve feed efficiency of pigs under commercial conditions.

Compensatory growth in pigs induced by Lys restriction may also be attributed to greater N retention (Ishida et al., 2015). Contrary to the previous phase, no difference was observed in N balance between pigs fed the CON or Lys-restricted diets in repletion phase 1. This result indicates that pigs subjected to early dietary Lys restriction may compensate for their N utilization, which could be positive from an environmental perspective by reducing the excretion of unused nutrients. Pigs undergoing a period of nutrient and energy restriction reach their maximum protein deposition (Pdmax) later (Martínez-Ramírez and de Lange, 2008). Thus, during refeeding, these animals prioritize protein deposition (PD), resulting in less energy available for lipid deposition (LD) when compared with pigs not previously exposed to restriction. In agreement, Martínez-Ramírez and de Lange (2008) reported that entire male pigs are able to partition a larger portion of available energy toward PD after Lys restriction is removed. This may explain the similar values of PD for all animals in repletion phase 1 and the lower final body lipid and LD in pigs previously fed Lys-restricted diets compared with those previously fed the CON diet. Indeed, Whang et al. (2003) suggested that Lys requirements for restricted pigs may be greater during the repletion phase because of their greater efficiency of protein utilization compared with pigs previously fed an adequate diet. In the current study, pigs previously fed the CON diet had greater

energy retained than those previously fed diets with greater levels of Lys restriction (i.e., Lys-28 and Lys-42 diets). Because fat deposition contains a greater energy value compared with protein gain (39.4 versus 23.5 kJ/g; Phillips et al., 1982), the greater energy retained in CON pigs may be explained by their greater LD.

Immunocastration is an alternative technique to surgical castration. The positive effects of immunocastration in entire pigs include improvements in growth performance (Pauly et al., 2009) and carcass characteristics (evidenced by a greater proportion of lean mass and lower fat thickness; Pesenti Rossi et al., 2022) when compared with barrows. Since Lys restriction and immunocastration may modulate pig responses, we expected that the effects of compensatory growth on growth performance and body composition observed in this study would also occur after the second dose of the immunocastration vaccine. Repletion phase 2 began immediately after the administration of the second dose of immunocastration and lasted 35 days. At the end of this phase, there was no difference in final BW among pigs. Indeed, the greater feed intake observed after the second dose may have helped previously Lys-restricted pigs to compensate for their BW during repletion phase 2. Although we did not include treatments with other categories (e.g., barrows or entire males) in this trial to confirm these suggestions, we are not aware of studies reporting complete catch-up in BW when Lys restriction exceeds 30%.

Pigs previously fed the CON diet had similar final body protein content to pigs previously fed the Lys-14 or Lys-28 diets and tended to have greater final body protein content than those previously fed the Lys-42 diet. As reviewed by Menegat et al. (2020), one of the conditions for compensatory growth in pigs is that Lys restriction ranges between 10% and 30% of the recommendations. The Lys-42 diet during the restriction phase corresponded to 58% of Lys requirements according to NRC (2012). Therefore, the tendency for greater final body protein content in pigs previously fed the CON diet compared with those fed the Lys-42 diet suggests that the degree of Lys restriction is a key factor that may induce permanent effects and prevent full compensatory growth. This may explain why pigs previously fed the Lys-42 diet showed a tendency to not fully recover in terms of protein composition.

Since our results showed that compensatory growth induced by Lys restriction had a positive impact on growth rate but not on body composition, further studies are warranted to better understand the response of immunocastrated male pigs under Lys restriction.

5. Conclusions

To conclude, our findings demonstrate that pigs fed the Lys-14 in the Lys-restricted phase were able to recover final BW and final body protein content already in the repletion phase 1 (entire male condition), whereas those pigs fed the Lys-28 diet recovered both variables in the repletion phase 2 (immunocastrated condition). Regarding the lowest Lys restriction evaluated (Lys-42), complete compensatory growth was observed only for the final body weight. These responses highlight interesting adaptive responses to Lys restriction and subsequent repletion, although they cannot be attributed solely to the previous Lys restriction. Diet formulation constraints may have influenced the AA balance and nutrient utilization, and these limitations should be considered.

Data availability

The entire database supporting this study was published in the article itself.

Author contributions

Conceptualization: Hauschild, L. **Data curation:** Silva, C. A.; Marçal, D. A. and Hauschild, L. **Formal analysis:** Silva, C. A. and Marçal, D. A. **Funding acquisition:** Lima, G. F. R. and Hauschild, L. **Investigation:** Silva, C. A. **Methodology:** Marçal, D. A. and Hauschild, L. **Project administration:** Lima, G. F. R. and Hauschild, L. **Resources:** Lima, G. F. R. and Hauschild, L. **Software:** Marçal, D. A. **Supervision:**

Hauschild, L. **Validation:** Marçal, D. A. and Hauschild, L. **Visualization:** Silva, C. A. **Writing – original draft:** Silva, C. A. and Fraga, A. Z. **Writing – review & editing:** Silva, C. A.; Marçal, D. A.; Fraga, A. Z.; Vieira, A. M.; Oliveira, M. J. K.; Valini, G. A. C.; Melo, A. D. B. and Hauschild, L.

Conflict of interest

The authors declare no conflict of interest.

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Declaration of generative AI in scientific writing

No AI tools were used, except for minor linguistic assistance in translating technical terminology.

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