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DIGESTIVE EFFICIENCY IN RABBIT DOES ACCORDING TO ENVIRONMENT AND GENETIC TYPE

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Abstract: Ninety lactating rabbit does of 3 different genetic types [2 from a line differentiating 20 generations by selection for litter size at weaning (V16 and V36) and 1 from a line founded under reproductive longevity criteria and then selected by litter size at weaning (LP)] were subjected to 3 environmental conditions: NC, females housed under normal conditions (14 to 20°C) and fed with a control diet [333 g neutral detergent fibre (NDF)/kg dry matter (DM)]; HC, females housed under heat conditions (25 to 35°C) and fed with the control diet; or NF, females housed under normal conditions and fed with a fibrous diet (443 g NDF/kg DM). The apparent digestible coefficients of dry matter (DMd), organic matter, crude protein (CPd), gross energy, NDF (NDFd) and acid detergent fibre, as well as the daily intake of DM, digestible protein and digestible energy (DE), were determined (14 to 18 d *post-partum*). The environment affected all variables analysed. In general, heat conditions reduced the daily DM intake (around –30%; $P<0.05$) and increased main apparent digestible coefficients (+4.5 percentage points for DMd). In contrast, the use of a fibrous diet led to reduce DE intake (–217 kJ/d; $P<0.05$) and main apparent digestibility coefficients (–13.5 percentage points for DMd). Females from line V, regardless of generation, showed lower daily DM intake (–19.2 g/d; $P<0.05$) and NDFd (–1.5 percentage points; $P<0.05$) than line LP. Interactions between genetic type and environment were found for daily DM intake, NDFd and CPd. When receiving fibrous diet, LP females showed a higher increment in daily DM intake (+65.6 g/d; $P<0.05$) than V36 females, compared to control. Under heat conditions, NDFd obtained for LP females were higher to those in normal conditions (+3.14 percentage points), while V females showed similar NDFd. In addition, the increase in CPd observed under heat conditions was higher for LP (+9.87 percentage points) and V36 (+8.74 percentage points) than V16 females (+3.84 percentage points). In conclusion, rabbit females from a line founded for reproductive longevity seem to show a higher flexibility in their digestive capacity under constrained conditions.

Key Words: rabbit does, heat stress, dietary energy, genetic selection, digestibility.

INTRODUCTION

Selection for litter size at weaning (LSW) in reproductive rabbit has not only succeeded in improving the target trait, but also changes important physiological aspects in the animals. In this sense, Quevedo *et al.* (2005) described a possible better efficacy in the digestible energy use for foetal growth and even an improvement in feed intake capacity at early lactation (Quevedo *et al.*, 2006), both changes directly related to the selection objective.

On the other hand, the foundation of a rabbit line by screening for females with very long reproductive career (Sánchez *et al.* 2008) resulted in animals with different capacity to manage

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the resources along their reproductive life. In fact, this strategy resulted in animals well adapted to manage the resources under adverse environmental conditions (i.e. high temperatures and feed restriction). They delayed reproductive senescence (Theilgaard *et al*., 2007) and improved their lifespan (Theilgaard *et al.,* 2006; Sanchez *et al.,* 2008), resulting in more robust animals (Theilgaard *et al.,* 2009). All of these findings could be related to a better use of the energy resources available to cope with the reproduction effort, as hypothesised by Pascual *et al.* (2008).

The current knowledge shows that maternal rabbit lines founded under different criteria but which had been selected for the same trait (i.e. LSW) are different for the selected trait (Ragab and Baselga, 2011), and previous works demonstrated that they adopted different fitness strategies when the environmental conditions were not at all suitable.

Therefore, the aim of the present work was to evaluate how selection for LSW (comparing animals separated by 20 generations of selection) or the foundation for hyper-reproductive longevity criteria could have affected female digestive efficiency under normal and constrained environmental conditions (heat or nutritional challenges).

MATERIALS AND METHODS

The experiment was designed and carried out according to the European Union recommendations on the protection of animals used for scientific purposes (European Union, 2010) and followed the guidelines for applied nutrition experiments in rabbits (Fernández-Carmona *et al*., 2005).

Animals

Ninety lactating rabbit females in first or second lactation were used to evaluate the apparent digestibility of animals belonging to 3 genetic types and kept under 3 different environmental conditions. The genetic types consisted of animals from a line founded under hyper-reproductive longevity criteria (see foundations details at Sánchez *et al.*, 2008) and then selected for LSW over 6 generations (line LP), and animals from line V, selected for LSW (Estany *et al.*, 1989) and belonging to generations 16 and 36 (V16 and V36, respectively).

Diets

Two diets differing in energy, mainly modifying the forage content, were formulated and pelleted (Table 1). The control diet (C) was formulated following the recommendations of de Blas and Mateos (2010) for lactating rabbit does [having on average 11.7 MJ of digestible energy (DE), 120 g digestible protein (DP), 168 g acid detergent fibre (ADF) and 333 g neutral detergent fibre (NDF) per kg dry matter (DM)]. A second fibrous low energy diet (F) was designed to induce a nutritional challenge (to have on average 9 MJ DE, 105 g DP, 266 g ADF and 443 NDF per kg DM).

Experimental procedure

At parturition, the rabbit does were housed in individual metabolic cages and randomly allocated to 1 of the 3 different environments resulting from the combination of environmental temperature and the diet received. Two room temperatures were used: a climatic chamber set up to obtain heat conditions (H) by means of a daily sigmoid temperature curve with a range from 25 to 35°C (see description by García-Diego *et al.*, 2011) and a normal conditions room (N) with a temperature range between 14 and 20°C. All animals housed at H received diet C while half of the animals placed at N were fed on diet C and half on diet F. As a result, the tested environments were

Table 1: Ingredients and chemical composition of the experimental diets.

Ingredients (g/kg)	Control diet (C)	Fibre diet (F)
Barley grain	315	0
Wheat bran	50	100
Sunflower meal (30% CP)	100	52
Soybean meal (44% CP)	101	0
Alfalfa hay	370	660
Sugar beet pulp	0	138
Soybean oil	40	10
L-Lysine HCl	0.45	2.8
DL-Methionine	0.95	2.6
L-Threonine	0.6	1.6
Arginine	0	0.8
Cycostat 66G®[1]	1	1
Bacipremix 50®[2]	2	2
Calcium carbonate	1	0
Dicalcium phosphate	10	0
Monosodium phosphate	0	21.2
Sodium chloride	4	4
Vitamin/mineral mixture[3]	4	4
Chemical composition (g/kg DM)		
Dry matter (DM; g/kg)	951	938
Organic matter	917	881
Neutral detergent fibre	333	443
Acid detergent fibre	168	266
Acid detergent lignin	25	44
Crude protein (CP)	175	162
Gross energy (MJ/kg DM)	18.69	18.31

[1] Alpharma, Antwerp (Belgium), provides 66 ppm of robenidine. [2] Andreés Pintaluba SA, Reus (Spain), provides 100 ppm of zinc bacitracin. [3] Contains (g/kg): thiamine, 0.25; riboflavin, 1.5; calcium pantothenate, 5; pyridoxine, 0.1; nicotinic acid, 12.5; retinol, 2; cholecalciferol, 0.1; α-tocopherol, 15; phytylmenaquinone, 0.5; cyanobalamin 0.0006; choline chloride, 100; $MgSO_4$ H_2O, 7.5; ZnO, 30; $FeSO_4$ $7H_2O$, 20; Cu SO_4 5 H_2O, 3; KI, 0.5; $CoCl_2$ 6 H_2O, 0.2; Na_2SeO_3, 0.03.

HC (heat conditions with diet C), NC (normal conditions with diet C) or NF (normal conditions with diet F). Table 2 summarises the experimental groups in terms of genetic type, environmental temperature and parturition order. Diets and water were provided *ad libitum* throughout the experiment, the daylight scheme was a 16 h light and 8 h dark period and the animals were artificially inseminated at day 11 *post-partum*.

Litters were standardised to 9 and 10 kits at first and second parturition, respectively, to compare the digestive efficiency at similar productive effort. Rabbit does were transferred daily to the production cage to suckle their respective litters. At 14 d of lactation, similar live weight were observed for the different animal types (on average 3 837±51 g), although females housed under heat conditions were slightly lighter (–197±73 g; $P<0.05$). Feed intake and faecal collections were recorded daily just after the milk production measurement (using the does double weight method) from the 14th to 18th day of lactation. This period was selected to perform the digestibility trial, as it corresponds to the period of maximum milk yield in rabbit does (Casado *et al*., 2006) and is characterised by a regular females' feed intake.

Table 2: Number of animals (*n*) according to environment condition and genetic type by parity order.

Environment [1]	HC			NC			NF		
Genetic type [2]	LP	V16	V36	LP	V16	V36	LP	V16	V36
Parity order									
First	5	6	6	5	6	6	6	5	5
Second	4	5	5	5	3	4	5	5	4
Total	9	11	11	10	9	10	11	10	9

[1] Environment: HC, heat conditions (25-35°C) and diet C (on av. 11.7 MJ digestible energy/kg dry matter); NC, normal conditions (14-20ºC) and diet C; and NF, normal conditions and diet F (on av. 9 MJ digestible energy/kg dry matter). [2] Genetic type: LP, line constituted for longevity-productive criteria; V16 and V36, line V selected by litter size at weaning during 16 or 36 generations.

The chemical analyses of diets and faeces for DM, crude protein (CP), ADF, acid detergent lignin (ADL) and ash followed the AOAC methods (934.01, 976.05, 973.18 and 942.05, respectively; AOAC, 2000). NDF was analysed by the method described by Mertens (2002) and the gross energy (GE) was determined in adiabatic bomb as recommended by EGRAN (2001).

Statistical analysis

Data on the apparent digestibility coefficients (d) of DM, organic matter (OM), CP, GE, NDF, ADF and insoluble hemicelluloses (HEM=NDF–ADF), as well as the daily intake of DM (DMI), DP (DPI) and DE (DEI), were analysed using the GLM procedure of SAS software (SAS Institute, 2009). The model included as fixed effects the genetic type (G_i, 3 levels), the environment (E_j, 3 levels) and their interactions. Although the trial was not designed to study the parturition order effect (PO_k, 2 levels), it was treated as a fixed effect, increasing the hypothesis test exigency. No interactions and no inference were performed with respect to PO_k. The model used was:

$$Y_{ijk}=G_i+E_j+PO_k+G_i\times E_j+e_{ijk}$$

To test the significances differences within genetic type or environment, different contrasts of interest were computed as follow:

LP *vs* V=(LPHC+LPNC+LPNF)/3–{[(V16HC+V16NC+V16NF)/3+(V36HC+V36NC+V36NF)/3]/2};
LP *vs*. V16=(LPHC+LPNC+LPNF)/3–(V16HC+V16NC+V16NF)/3;
LP *vs*. V36=(LPHC+LPNC+LPNF)/3–(V36HC+V36NC+V36NF)/3;
V16 *vs*. V36=(V16HC+V16NC+V16NF)/3–(V36HC+V36NC+V36NF)/3;
HC *vs*. NC=(LPHC+V16HC+V36HC)/3–(LPNC+V16NC+V36NC)/3;
and NF *vs*. NC=(LPNF+V16NF+V36NF)/3–(LPNC+V16NC+V36NC)/3.

Finally, for variables where $G_i\times E_j$ interaction was declared significant, the means comparisons were performed using a t-test.

RESULTS AND DISCUSSION

The environment affected all the variables studied (Table 3). Animals submitted to the heat challenge (HC) showed a lower DMI, DPI and DEI (34.3, 24.3 and 29.6%, respectively; $P<0.05$), while their main apparent digestibility coefficients (DMd, OMd, CPd, GEd and ADFd) increased (from 4 to 7 percentage points; $P<0.05$) in comparison to animals kept at NC. As recently reviewed by Cervera and Fernández-Carmona (2010), high temperatures usually depress feed intake of rabbits and consequently increase the apparent digestibility coefficients

Table 3: Apparent digestible coefficients [dry matter (DMd), organic matter (OMd), crude protein (CPd), gross energy (GEd), neutral detergent fibre (NDFd), acid detergent fibre (ADFd) and insoluble hemicellulose (HEMd)] and daily intake [dry matter (DM), digestible protein (DP) and digestible energy (DE)] according to environment and genetic type of females on lactation (from 14 to 18 d).

Environment[1]	HC			NC			NF			Contrast[3]					
Genetic type[2]	LP	V16	V36	LP	V16	V36	LP	V16	V36	LP*vs.*V	LP*vs.*V16	LP*vs.*V36	V16*vs.*V36	HC*vs.*NC	NF*vs.*NC
Apparent faecal digestibility coefficients (%)															
DMd	67.85^{d}	65.64^{c}	66.50^{cd}	61.90^{b}	63.03^{b}	61.52^{b}	48.25^{a}	49.02^{a}	48.67^{a}	0.27 (0.45)	0.10 (0.51)	0.44 (0.51)	0.33 (0.51)	4.51* (0.51)	−13.51* (0.52)
OMd	68.37^{d}	66.47^{c}	67.16^{cd}	62.95^{b}	64.08^{b}	62.74^{b}	48.90^{a}	49.58^{a}	49.40^{a}	0.17 (0.43)	−0.03 (0.50)	0.30 (0.50)	0.27 (0.50)	4.07* (0.50)	−13.96* (0.50)
CPd[4]	77.35^{d}	74.73^{d}	75.57^{d}	67.48^{b}	70.89^{c}	66.83^{b}	63.29^{a}	64.83^{ab}	65.10^{ab}	−0.28 (0.81)	−0.78 (0.93)	0.21 (0.94)	0.99 (0.94)	7.48* (0.93)	−3.99* (0.95)
GEd	67.80^{c}	66.03^{c}	66.52^{c}	62.33^{b}	63.29^{b}	61.74^{b}	48.92^{a}	49.84^{a}	49.83^{a}	0.14 (0.49)	−0.04 (0.56)	0.32 (0.56)	0.36 (0.56)	4.32* (0.56)	−12.93* (0.57)
NDFd[4]	31.50^{d}	28.01^{c}	27.43^{bc}	28.36^{c}	28.55^{c}	26.59^{abc}	24.56^{a}	24.40^{a}	25.03^{ab}	1.47* (0.65)	1.15 (0.75)	1.79* (0.75)	0.64 (0.75)	1.15 (0.76)	−3.17* (0.76)
ADFd	21.15^{d}	18.90^{cd}	16.89^{bc}	13.48^{a}	14.34^{ab}	13.89^{ab}	17.33^{c}	17.50^{c}	17.72^{c}	0.78 (0.77)	0.40 (0.88)	1.15 (0.90)	0.75 (0.89)	5.08* (0.90)	3.61* (0.90)
HEMd	43.36^{d}	38.44^{bc}	39.47^{c}	43.55^{d}	43.11^{d}	41.24^{cd}	35.40^{a}	34.72^{a}	36.00^{ab}	1.94* (0.73)	2.01* (0.84)	1.86* (0.85)	−0.15 (0.84)	−2.21* (0.85)	−7.26* (0.85)
Daily intake															
DM (g /d)[4]	208.1^{a}	194.2^{a}	217.6^{a}	316.3^{b}	299.5^{b}	327.5^{bc}	415.4^{e}	367.5^{d}	358.0^{dc}	19.2* (8.5)	26.2* (9.9)	12.2 (9.9)	−14.0 (9.9)	−107.8* (9.9)	65.9* (9.9)
DP (g /d)	28.16^{a}	25.30^{a}	28.73^{a}	37.11^{b}	37.13^{b}	38.27^{b}	42.56^{c}	38.65^{bc}	38.84^{bc}	1.46 (1.1)	2.25 (1.2)	0.67 (1.2)	−1.58 (1.2)	−10.11* (1.2)	2.51* (1.2)
DE (kJ /d)	2 642^{a}	2 393^{a}	2 706^{a}	3 675^{cd}	3 541^{bcd}	3 778^{d}	3 720^{d}	3 355^{bc}	3 267^{b}	172.6 (95)	249.6* (110)	95.6 (110)	−154.0 (110)	−1084.7* (110)	−217.4* (111)

[1] Environment: HC, heat conditions (25-35°C) and diet C (11.7 MJ digestible energy/kg DM); NC, normal conditions (14-20°C) and diet C; and NF, normal conditions and diet F (9.0 MJ digestible energy/kg DM). [2] Genetic type: LP, line constituted for longevity-productive criteria; V16 and V36, line V selected by litter size at weaning during 16 or 36 generations. [3] Contrast within genetic type or environment were calculated on complete data; *e.g.* LP *vs.*V=(LPHC+LPNC+LPNF)/3−{[(V16HC+V16NC+V16NF)/3 +(V36HC+V36NC+V36NF)/3]/2}. [a, b, c, d] Means not sharing superscripts, in rows, are different at $P<0.05$. Contrasts (standard error) followed by * are significant at $P<0.05$. [4] Interaction environment×genetic type significant ($P<0.05$).

of main nutrients. A decrease in the amount of feed eaten normally leads to a lower passage rate, hence the ingested feed is exposed to the action of digestive enzymes for a longer period, thereby increasing digestibility of nutrients (Carabaño *et al.*, 2010).

The only nutrient whose apparent digestibility coefficient not increased at high environmental temperature was insoluble hemicellulose (HEM 40.6 and 42.4% for HC and NC groups, respectively; $P<0.05$). This discordant response is difficult to explain from our results. In any case, Gidenne *et al.* (2002), and Gidenne and Feugier (2009) described similar bacterial fibrolytic activity independently of the feed intake level, suggesting that digestibility of some cell-wall constituents is not substrate-dependent. Moreover, Hannah *et al.* (1990) observed that NDF digestibility was also similar in sheep housed at 27 to 34°C.

On the other hand, animals at NF showed higher DMI and DPI (17.3 and 6.6%, respectively; $P<0.05$) and a reduction in the digestibility (DMd, OMd, CPd, GEd and NDFd; $P<0.05$) except for ADFd, which was higher (3.6 percentage points; $P<0.05$) compared to those at NC. DMI, clearly increased by the use of a high fibre low energy diet during lactation, agrees with the literature (Fernández-Carmona *et al.,* 1995, 2003; Quevedo *et al.,* 2006; Nicodemus *et al.,* 2010), where the response on DMI was related to the dietary DE content. On average, DMI of lactating rabbit does increased about 8% per each MJ of DE decreased in the diet. In spite of this, the DE content of the diet F (about 9.0 MJ/kg DM) did not allow females to compensate the DE intake completely (5.9% lower compared to control; $P<0.05$).

The reduction of DMd, OMd and GEd (13-14%) in diet F mainly reflects the change in carbohydrate composition, higher fibre and lower starch than diet C, as well as the effect of increased DMI. However, NDFd and ADFd were less affected by the dietary change. The design of a high fibre diet by changing the forage content also involved a change in the fibre sources (Table 1) and, consequently, in the nature of fibre constituents, and this also affected the digestibility of fibre fractions (Gidenne *et al.,* 2010). Moreover, the higher addition of unsaturated oil in diet C could have affected its fibre digestibility (Fernández *et al*., 1994).

Regarding the genetic type, a higher DMI was observed for LP in comparison to V16 animals (+26.2 g DM/d; $P<0.05$) whereas compared to V36 animals it was similar (+3.9%). Similarly, DEI was higher for LP than for V16 animals (3 345.8±77.9 and 3 096.2±78.1 kJ/d, respectively; $P<0.05$). Moreover, the NDFd was higher (1.4%; $P<0.05$) for LP than for V36 animals (+1.8%, $P<0.05$). As observed by Pascual *et al.* (2008) and Theilgaard *et al.* (2009), females from LP line showed a higher feed intake (19.21 g DM/d) during lactation period than the V line. However, the difference between V16 and V36 (–14.0 g DM/d) was not statistically significant.

Interactions between genetic type and environment were observed for DMI, NDFd and CPd. DMI of LP animals was significantly higher compared to V16 and V36 animals, but only when fed with diet F (+47.9±16.6 and +57.4±17.1 g DM/d, respectively; $P<0.05$) (Figure 1a). Furthermore, the higher NDFd observed for LP animals was mainly due to the increase observed under heat challenge (HC) relative to normal room temperature (NC) (+3.1±1.3 percentage points; $P<0.05$), which was not observed for V animals (Figure 1b).

In the current study, only the NDFd was higher for the LP line, relative to line V. However, Pascual *et al.* (2008) observed better digestibility of DM, OM and GE in favour of line V. This difference in the NDFd in the present study did not seem to be a direct response to differences in feed intake, because the highest NDFd occurred in animals submitted to a heat challenge (Table 3), where feed intake was similar among genetic types (208.0±12.7, 194.2±11.5 and 217.6±11.5 g DM/d for LP, V16 and V36, respectively). In fact, the reduction in DMI of line LP

at HC to similar levels of line V could explain these results, because the passage rate would also decrease, promoting an increase in fibre digestibility. Generations 16 and 36 of line V presented similar raw results for this variable, but a possible different pattern in restricted environments (especially at high temperatures) should be confirmed.

Finally, Figure 1c shows the genetic-type×environment interaction for CPd as changes due to heat and nutritional challenges (HC and NF, respectively) compared to NC. Heat challenge led LP animals to an increase of CPd significantly higher than that observed for V16 animals (9.9±1.6 *vs.* 3.8±1.6 percentage points, respectively; $P<0.05$), with V36 animals showing an intermediate increment (8.7±1.6). However, in NF environment, V16 showed a greater reduction on CPd (–6.1±1.7 percentage points; $P<0.05$), while V36 females did not seem to be affected when fed with diet F (–1.7±1.7 percentage points) compared to NC environment. Females from line LP showed an intermediate reduction in CPd with diet F (–4.2±1.6%) compared to diet C.

The genetic type fixed effect *per se* did not affect the CPd but the environment did (+7.5 % under heat challenge and –4.0% for a high fibre-low energy diet). However, there was a significant genetic type×environmental interaction. Generation 16 of line V presented a high CPd at NC compared to generation 36 and line LP (+6.6%; $P<0.05$). However, under the constrained environment, this difference disappeared, which suggests that line LP and generation 36 of line V adjusted the CPd better in unfavourable conditions. Theilgaard *et al.* (2007 and 2009) described the flexibility of LP line, especially in constrained environments and later in productive life. In summary, the LP line seems to have a greater ability to obtain resources when the environment is not suitable, which is manifested in its higher DMI, when fed a high fibre low-energy diet (NF), in the better digestibility of fibre under

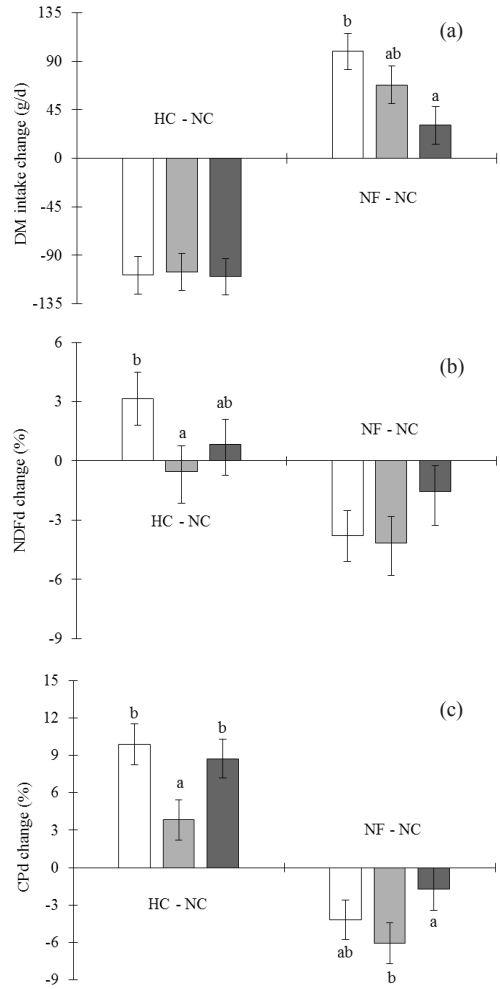

Figure 1: Change on (a) dry matter intake, (b) apparent digestibility coefficients of neutral detergent fibre and (c) crude protein caused by the heat (HC–NC) or nutritional (NF–NC) challenges respect to the control conditions for the different genetic types (□ LP, ▒ V16 and ■ V36). LP: line constituted for longevity-productive criteria; V16 and V36: line V selected for litter size at weaning during 16 and 36 generations. HC: heat conditions (25-36ºC) and diet C (11.7 MJ digestible energy/kg DM); NC: normal conditions (14-20ºC) and diet C; and NF: normal conditions and diet F (9 MJ digestible energy/kg DM)]. Error bars represent the standard errors. [a, b]: means for the different genetic types on same environment not sharing letters were significant different ($P<0.05$).

heat stress (HC), and the advantage in CPd (both under HC and NF environment). All of this suggests that the foundational criteria applied to line LP also selected animals with a greater digestive flexibility.

On the other hand, digestive efficiency of females did not seem to be affected after 20 generations of selection for litter size. Although females more selected for this criteria could have increased their ability to obtain resources at the beginning of lactation, as observed by Quevedo *et al.* (2006), and which could be also guessed from our results, digestive efficiency for main nutrients was not changed to any great extent. However, the higher DEI reduction of more selected animals under a nutritionally constrained environment (NF) could be related to a higher sensitivity to that environment, which must be studied in further works.

CONCLUSIONS

Both heat and the nutritional challenges affected the feed intake (reduction and increasing, respectively) and consequently the apparent digestible coefficients (improved and decreased, respectively). The selection over 20 generations for litter size at weaning was not a factor improving the feed intake capacity or the digestibility of the animals, but did improve the flexibility under constrained conditions. The foundation criteria for long-productive animals followed by a selection for litter size at weaning was effective, improving the feed intake capacity without reducing the digestive capacity and flexibility under constrained conditions. These patterns seem to contribute to a longer productive lifespan.

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