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A moderate protein diet does not cover the requirements of growing rabbits with high growth rate

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Abstract

Genetic selection for feed efficiency has increased the growth rate and requirements of growing rabbits, while the protein content of commercial feeds has been adjusted to avoid digestive disorders. The aim of this work was to evaluate how a diet with moderate levels of protein [146 g crude protein (CP)/Kg] could be affecting protein and amino acids acquisition in terms of growth rate of the animals. From 189 weaned rabbits (28 days old), only 41 animals were selected at 42 days, in order to ensure the greatest variability for growth rate during fattening. To achieve this goal, animals came from three genetic lines: H and LP (maternal lines selected by litter size) and R (paternal line selected for growth rate), characterised by normal, moderate and high growth rate during the fattening period, respectively. Apparent faecal digestibility of dry matter (DM), CP and gross energy (GE) of the diet from 49 to 53 days of age, as well as the ileal apparent digestibility of DM, CP and amino acids at 63 days of age, was determined in all the selected animals. Protein, energy and amino acids retained in the empty body during the fattening period were also determined by slaughtering 15 weaning rabbits at 28 days, and the 41 selected animals at 63 days of age. Animals from the R line showed higher feed intake than those from maternal lines, as well as lower feed conversion ratio, even below that expected from their growth rate.

Apparent faecal digestibility of GE and apparent ileal digestibility of DM, CP and cystine of the diet were higher in LP than in H rabbits ($P<0.05$), showing intermediate values in R rabbits. However, apparent ileal digestibility of glutamic acid and glycine was significantly higher in R than in H rabbits ($P<0.05$), showing intermediate values in LP rabbits. As expected, both daily protein and energy retained in the empty body increased as growth increased. However, R growing rabbits seem to have lower protein retained and higher energy retained in the empty body than that expected from their growth. In fact, protein to energy retained ratio was clearly lower for R growing rabbits. These results seem to show the possible existence of some limiting amino acid when current moderate protein diets are used in growing rabbits with high growth rates, recommending a review of the amino acid requirements for the growing rabbits from paternal lines.

Key words: Rabbit, growth rate, protein, amino acids, retention and digestibility.

Abbreviations used:

ADF: acid detergent fibre

ADG: average daily gain

CP: crude protein

DFI: daily feed intake

DM: dry matter

DP: digestible protein

DPI: digestible protein ingested

DPr: digestible protein retained

EBWG: empty body weight gain

FCR: feed conversion ratio

GE: gross energy

LW: live weight

NDF: neutral detergent fibre

SAS: Statistical analysis system

Introduction

There is a need to reduce feeding costs in rabbit farms by improving feed conversion ratio (FCR), and paternal lines, designed to improve feed efficiency, play a relevant part in achieving this goal (Cartuche et al., 2014). Usually, selection for feed efficiency in current rabbit genetic programmes is done indirectly, selecting average daily gain (ADG), as there is a negative genetic correlation between these two traits (Blasco, 1989; Baselga, 2004). Currently, the animals from these parental lines show ADG values above 55 g/day during the fattening period (Marín-García et al., 2016).

Commercial feeds for growing rabbits are designed to ensure an adequate ADG for three-way crossbred animals [usually with crude protein (CP) levels over 150 g/Kg]. In any case, Carabaño et al. (2009) reported that protein levels around 140 g/Kg did not impair growth performance in growing rabbits with ADG rates of up to 55 g per day. However, since the onset of epizootic rabbit enteropathy, the protein content of commercial feeds has been decreased (to moderate levels of 140-150 g/Kg) to reduce the risk of digestive troubles (Trocino et al., 2013). In this context, animals with a high ADG could have difficulties proving their growth potential with those diets.

Genetic progress in the paternal rabbit lines for feed efficiency may be due to different improvements in utilisation of the feed nutrients, e.g. an improvement in the digestive efficacy at the ileal (or even faecal) level, or higher efficiencies in use of the digested nutrients for maintenance or growth. In growing rabbits, part of the digestible protein ingested (DPI) is used to cover the maintenance requirements [2.13 g DP day $^{-1}$ kg $^{-1}$ live weight (LW)$^{0.75}$; Lv et al., 2009] and a second part is retained in the body (DPr; with an estimates DPr/DPI efficiency of 0.56; Partridge et al., 1989). However, as these processes are not completely efficient, a fraction of the DPI, together with the renewed amino acids of the maintenance, is used in the oxidative degradation of the amino acids as energy source and excreted in the form of urea. The lower this latter fraction, the greater the efficiency of the rabbits in use of the DPI. In any case, independently of their possible efficacy improvement, animals with a higher growth rate would also have higher requirements for maintenance (due to their higher live weight) and for growth (due to their higher ADG), and there will possibly be a greater amount of DPI that will be used as an energy source. For all these reasons, high growth rate animals should have a greater protein input than animals with lower growth, as otherwise protein retention and their growth could be penalised.

Pascual et al. (2008), comparing growing rabbits from a paternal line that differed in 11 generations of selection for ADG, and given a feed with 161 g CP/Kg, observed that there were no significant differences in relative growth of any of the body components studied, with both genetic types showing similar growth patterns and carcass composition. However, Pascual et al. (2007), when comparing growing rabbits that differed in 16 generations of selection for ADG, but given a feed with 145 g CP/Kg, observed that the most selected animals had greater dissectible fat percentage and lower meat to bone ratio of the hind leg. These results lead us to hypothesise that when diets with a moderate protein content are used, growing rabbits with a high growth rate may not be able to correctly cover their protein requirements, which may be affecting the correct elaboration of the rankings and genetic progress in the paternal lines.

Therefore, the aim of this work was to evaluate how a current commercial growing rabbit diet, with moderate levels of digestible protein, could be affecting protein and amino acids acquisition (considering both their digestibility and retention) depending on the growth rate of the animals (using genetic lines differing for this trait).

Material and methods

The experimental procedure was approved by the Animal Welfare Ethics Committee of the Universitat Politècnica de València and carried out following the recommendations of the European Group on Rabbit Nutrition (Fernández-Carmona et al., 2005). The experimental protocols followed the Spanish Royal Decree 53/2013 on the protection of animals used for scientific purposes [Boletín Oficial del Estado, 2013],

Animals

One-hundred and eighty-nine weaned rabbits (28 days old), from three genetic lines (H, LP and R) developed at the Institute of Animal Science and Technology of the Universitat Politècnica de València, were used, in order to ensure a wide range for the growth rate of the rabbits during the fattening period (58 animals from each genetic line). These lines differ greatly in their genetic background and growth rate during the fattening period. Line H, which was founded following hyper-prolific criteria at birth (Cifre et al., 1998) and selected by litter size at weaning over 17 generations, is characterised by a large litter size at weaning but a normal growth rate during the growing period. Line LP, founded by hyper-longevity criteria (Sánchez et al., 2008) and selected by litter size at weaning off our 7 generations, is characterised by a greater robustness than other lines and good growth rate during the growing period. Finally, Line R, which was obtained after two generations of randomly mating from a pool of animals of three commercial sire lines (Estany et al., 1992), and then selected by ADG in the growing period over 38 generations, is characterised by a high growth rate during the growing period.

Diet

Table 1 shows the ingredients and chemical composition of the experimental diet used in this work. The feed was formulated to be a moderate protein diet [but ensuring the minimum recommendations for DP (111 g/Kg dry matter (DM)) and the main essential amino acids (8.3, 5.7 and 6.9 g of lysine, sulphur amino acids and threonine per Kg DM, respectively), as proposed by de Blas and Mateos (2010). A version of the diet including 5 g/Kg DM of alfalfa hay marked with ytterbium was also manufactured.

Experimental procedure

Throughout the experimental period (February to March), animals were kept at 15ºC to 22ºC, with a photoperiod of 16 hours of light and 8 hours of darkness. At 28 days of age, 15 weaned rabbits (5 per genetic line) were slaughtered by intracardiac puncture with sodium thiopental (75 mg/Kg of LW) to determine the empty body characteristics at 28 days of age. The rest of the animals were housed in individual cages and fed with the experimental diet until 63 days of age. Mortality and morbidity (presence of diarrhoea) were controlled daily and feed intake and LW were recorded weekly. Any animal presenting any digestive anomaly, weight loss or low ingestion was automatically ruled out of the trial. At 42 days of age, from the total of growing rabbits, 50 were initially selected for the trial (15, 18 and 17 of the H, LP and R lines, respectively), although only 41 of these animals -without any anomaly- gave us complete information at the end of the trial (11, 17 and 13 of the H, LP and R lines, respectively). The initial selection criteria within genetic type consisted of choosing those animals that could provide the greatest variability in growth rate during fattening, based on the animals' ADG shown in the first two weeks (28 to 42 days of age).

At 42 days of age, selected animals were housed in individual metabolic cages of 52×44×32 cm and, after a week of acclimatisation, a faecal digestibility trial was conducted. From 49 to 53 days of age, feed consumption was controlled and faeces produced were collected. Faeces were stored in identified plastic bags and frozen at −20ºC until analysis. Apparent faecal digestibility coefficients for DM, CP and gross energy (GE) were determined for each animal. From 53 days of age, all the animals began to receive the feed marked with ytterbium until their slaughter at 63 days of age. At this age, animals were weighed and slaughtered by intracardiac injection of sodium thiopental (75 mg Kg^{-1}LW) between 19:00 to 23:00 h, to minimise the influence of caecotrophy on the composition of digestive contents (Merino and Carabaño, 2003). Samples of ileal content were taken from the distal part of the small intestine (around 20-40 cm before the ileo-caeco-colic valve) for each animal, frozen at –20ºC, freeze-dried and ground. The whole digestive tract was emptied and reintroduced into the body of the dead animal. Empty bodies, obtained at 28 and 63 days of age, were weighed and placed in plastic bags, identified and frozen at –40ºC. Frozen empty bodies were crushed and homogenised in a cutting machine (Tecator, Abusson, France), and one sample per animal was freeze-dried and stored at –40ºC until analysis.

Chemical analysis

Feed was analysed for DM, ash, CP, neutral detergent fibre (aNDFom), acid detergent fibre (ADFom), lignin (sa), starch, GE and amino acid content. Faeces were analysed for DM, CP and GE, and ileal samples for DM, CP, and amino acid content. Finally, empty bodies samples were analysed for DM, CP, GE and amino acid content. Samples were analysed according to the methods of AOAC (2000): 934.01 for DM, 942.05 for ash and 976.06 for CP. Starch content was determined according to Batey (1982). The aNDFom (assayed with a thermo-stable amylase and expressed exclusive of residual ash,), ADFom (expressed exclusive of residual ash) and lignin (determined by solubilisation of cellulose with sulphuric acid, sa) were analysed sequentially (Van Soest et al., 1991). GE was determined by adiabatic bomb calorimetry (Gallenkamp Autobomb, Loughborough, UK).

The amino acid content was determined after acid hydrolysis with HCL 6N at 110◦C for 23h as previously described by Bosch et al. (2006), using a Waters (Milford, Massachusetts, USA)

HPLC system consisting of two pumps (Mod. 515, Waters), an autosampler (Mod. 717, Waters), a fluorescence detector (Mod. 474, Waters) and a temperature control module. Aminobutyric acid was added as internal standard after hydrolysation. The amino acids were derivatised with AQC (6-aminoquinolyl-N-hydroxysuccinimidyl carbamate) and separated with a C-18 reverse-phase column Waters AcQ Tag (150 mm × 3.9 mm). Methionine and cystine were determined separately as methionine sulphone and cysteic acid, respectively, after performic acid oxidation followed by acid hydrolysis (Alagon et al., 2016).

Statistical analysis

From the information obtained from those weaned rabbits slaughtered at 28 days of age (empty body weight and CP, GE and amino acids contents in the empty body), there were fitted regression equations including LW at 28 days of age as dependent variable for each of them. Values for all these variables at 28 days of age for the animals slaughtered at the end of retention trial (63 days of age) were estimated for each animal by means of these equations to properly determine nutrient retention during the growing period.

Data on performance traits (growth, intake and FCR), apparent digestibility coefficients (both faecal and ileal) and nutrients retained in the empty body of the animals (protein, energy and amino acids) were analysed using a GLM model from SAS (Statistical Analysis System), including the genetic type as the only fixed effect. In the case of apparent digestibility coefficients and nutrients retained in the empty body, lineal effect of ADG or daily empty body weight gain (EBWG) were also respectively determined.

The evolution of daily feed intake (DFI), FCR, protein and energy retained, and protein to energy retained ratio according to the daily EBWG of animals were evaluated. As the moderate protein diet used in this work should theoretically meet the requirements of the animals coming from the maternal lines (H and LP), lineal regressions for these variables with EBWG were obtained by fitting only the data from the maternal lines. Lineal regressions were obtained using REG procedure of SAS, extrapolating to high EBWG values. Finally, other relationships of interest with the EBWG, such as the proportion of digestible protein intake addressed to different life functions or the total protein ingested, retained, used in maintenance or not used, were determined with a REG procedure of SAS using all the animals’ data.

Results

Table 2 shows the data on the main performance traits controlled in this work. Through the use of various genetic types and the choice of animals from a larger population at 42 days of age, the data set used in this study showed a wide range for most of the performance traits. In fact, high coefficients of variation for growth traits (20 to 25%), feed intake (18%) and FCR (8%) were obtained. Regarding the effect of the genetic type, LW at 63 days of age of the R line rabbits was higher than for those of the LP line (+741 g; $P<0.05$) and that of the LP higher than those of the H line (+222 g; $P<0.05$). In addition, DFI, ADG, EBWG and FCR of growing rabbits of R line was significantly higher than those obtained for LP and especially H line (on av. +40 g/day, +22 g/day, +19 g/day and –0.28, respectively; $P<0.05$).

Figure 1 shows the effect of EBWG during the growing period on average DFI and FCR observed for the rabbits. Growing rabbits from R line showed higher DFI compared with those of maternal lines (+35%; $P<0.001$), but the effect of genetic type disappeared when ADG was included as a covariate. In addition, animals from the R line showed lower FCR than those from maternal lines (+11%; $P<0.001$), and differences were maintained when covariate ADG was included in the model. These effects could be also deduced from the extrapolated regression lines obtained with the DFI and FCR data from maternal lines, which show how R growing rabbits seem to have a slightly lower DFI, but a clearly lower FCR than that expected from their EBWG.

The effect of genetic type or ADG on the main coefficients of apparent faecal and ileal digestibility are presented in Table 3. Apparent faecal digestibility of GE and apparent ileal digestibility of DM, CP and cystine were significantly higher in LP than in H rabbits (+0.019, +0.125, +0.076 and +0.140, respectively; $P<0.05$), showing intermediate values in R rabbits. However, apparent ileal digestibility of glutamic acid and glycine were significantly higher in R than in H rabbits (+0.051 and +0.152, respectively; $P<0.05$), showing intermediate values in LP rabbits.

Protein and amino acids retained in the empty body depending on the genetic type of growing rabbits are shown in Table 4. As expected, total daily protein retained increased with the growth rate (+0.145 g of protein for each +1 g/day in the EBWG; $P<0.05$), with R rabbits showing greater daily protein retention than LP rabbits (+1.9 g/day; $P<0.05$), and these latter greater than H rabbits (+0.9 g/day; $P<0.05$). However, the amount of protein retained per unit of empty body was significantly lower in R than in LP and H rabbits (on av. –20 mg per g of empty body), a significant lineal decrease of protein being retained per unit of empty body as the daily EBWG increased (–0.95 mg for each +1 g/day in the EBWG; $P<0.05$). Similarly, the amount of glutamic acid and sulphur amino acids in the empty body was lower in R than in LP and H rabbits ($P<0.05$). The amount of alanine, aspartic acid, cysteine, histidine, lysine, threonine and valine in the empty body was significantly lower in R than in LP rabbits ($P<0.05$). For all these amino acids cited, we observed a lineal decrease in their retention per unit of empty body as the daily EBWG increased (from –0.14 to –0.02 mg for each +1g/day in the EBWG $P<0.05$).

Finally, Figure 2 shows the evolution of daily protein and energy retained in the empty body, as well as their ratio, according to the daily EBWG of growing rabbits. As expected, both daily protein and energy retained in the empty body increased as the daily EBWG increased (Figure 2a). However, when regression lines were obtained with the data from maternal lines and extrapolated, R growing rabbits seem to have lower protein retained and higher energy retained in the empty body than that expected from their EBWG. In fact, protein to energy retained ratio was clearly lower for R growing rabbits (Figure 2b).

Discussion

The main aim of this work was to determine whether growing rabbits with a high growth rate are able to correctly cover their protein requirements when the current diets with a moderate protein content are used. This condition is very important for the correct elaboration of the genetic rankings in the paternal lines, which could significantly affect the efficiency in rabbit farms. To assess this fact, we have built a population of growing rabbits with a wide ADG using three different genetic types, which a priori should differ in this parameter. This premise has been achieved, providing a population distributed homogeneously from 34 to 70 g/day of ADG and from 26 to 65 g/day of EBWG. In fact, the differences found in growth traits among the different genetic types, although affected by the initial selection of the animals, showed the expected behaviour for these genetic types. R growing rabbits showed greater DFI and ADG and lower FCR than H ones, with LP animals presenting intermediate values. These results agree with those obtained for these same lines by García-Quirós et al. (2014) and Mínguez et al. (2016).

As expected, feed intake was highly correlated with the growth rate of the animals (increasing 2.5 units DFI per unit of EBWG) independently of the genetic type. However, although feed efficiency improved as the growth rate of animals increased, animals from line R seems to show a lower FCR than expected. The regression lines of Figures 1 and 2 were obtained only with the data of the animals from the maternal lines, with a growth rate below 45 g/day, as the diet offered should easily cover the requirements of these animals (Carabaño et al., 2010), and the growing rabbits from the R line had much lower FCR than expected from this projection (on av. –0.21 points). Although an increase in the ADG leads indirectly to the improvement of FCR, there are other factors such as the criteria of foundation (Savietto et al., 2014) or the continued genetic selection for ADG of this line, which could explain the greater effectiveness of these animals.

A possible explanation for the improvement in the FCR could be an improvement in the digestive efficiency of the animals that show a higher growth rate. However, ADG of animals did not affect the apparent digestibility coefficients of all the nutrients controlled, but growing rabbits of the line H showed a worse utilisation of the dietary DM, GE, CP and some amino acids than those from LP and R line. Savietto et al. (2012) found that rabbit females from the LP line seem to show a higher flexibility in their digestive capacity under constrained conditions, presenting greater faecal digestibility coefficients for aNDFom and CP than those females from other maternal lines. However, according to this hypothesis, R rabbits should have shown greater efficiency in the digestive utilisation of nutrients than LP rabbits, as they show a clearly greater growth rate. Perhaps the digestibility of the nutrients in animals with very high growth rate could penalised due to associated high feed intake. An increase in the amount of feed eaten normally leads to a higher passage rate, hence the ingested feed is exposed to the action of digestive enzymes for a shorter period, thereby decreasing the digestibility of nutrients (Carabaño et al., 2010). In any case, differences in digestive efficiency observed in this study seem to be more related to the genetic type used than to growth rate.

As expected, the greater the digestible protein intake, the greater was the daily protein retained in the empty body of the rabbits during the fattening period. Therefore, a positive lineal relationship between daily EBWG and the daily protein retained was observed. Although there are not many studies where the effect of growth rate on protein retention has been studied, an increase in ADG is always associated with an increase in the total amount of protein retained in the body (Gidenne and Perez, 2000; Birolo et al., 2016). However, the animals of the R line showed a lower content of protein retained per unit of empty body than the animals from the H and LP lines, as well as for some amino acids among which are some essential amino acids identified as limiting in the growing rabbit diets (lysine, sulphur amino acids and threonine). Armero (1998) already reported in pigs that the content of some amino acids in muscle could be different depending on genetic type. Although there is a global negative linear correlation between the growth rate and protein and amino acid content retained in the empty body, this effect is only advisable in animals of the R line, but not in H and LP lines, where a diet with a moderate protein level would have no difficulties in covering the requirements correctly. These results could be showing that, when diets with a moderate level of protein are used, some amino acids could be limiting the correct development of animals with high growth from paternal lines.

In fact, in Figure 2 we can see this issue in a more graphic way. Rabbits from maternal lines linearly increase the daily amount of protein retained as their growth rate increases. However, when the animals have a growth rate above 50 g/day of ADG (approx. 43 g/d of EBWG), these rabbits from R line show a lower protein retention than expected from their growth rate. These animals, with a high growth rate, would show a lower protein deposition than expected when fed with moderate protein diets, possibly due to the presence of some amino acid limiting the protein synthesis. In this way, the remaining excess amino acids would be derived for their use as energy source (Leningher et al., 1983), which would be deposited in the form of body fat in the animal. In fact, these animals showed a greater amount of energy retained in the body, as well as a clearly lower protein/energy ratio retained than that expected for their growth rate. These results would be in agreement with those observed by Pascual et al. (2007 and 2008) when analysing the body composition of growing rabbits from R line that only differed in their degree of selection (16 and 11 generations of difference, respectively), and therefore in their growth rate. Pascual et al. (2008), using a feed with 161 g CP/Kg that should theoretically cover the protein requirements of high growth rate animals, observed that there were no significant differences in relative growth of any of the body components studied, with both generations showing similar growth patterns and carcass composition. However, Pascual et al. (2007), using a feed with 145 g CP/Kg close to that used in the present work and the current commercial feeds, observed that the most selected animals had greater dissectible fat percentage and lower meat to bone ratio. These results would confirm the hypothesis of the existence of some limiting amino acid in animals with high growth rate when the current fattening feeds with moderate levels of protein are used.

However, if animals from R line did not have a better digestive efficiency in the use of nutrients, and protein retention is lower than expected, why do they show a better FCR than expected for their growth rate? To answer this question, we shall use Figure 3, which shows the utilisation of the protein and the proportion of the DP ingested addressed to the different vital functions of the animal depending on the animals' growth rate. As expected, the greater the protein ingestion, the faster the animals' grow and the greater the amount of protein that is addressed to maintenance and growth (Figure 3a). However, the proportion of protein addressed for maintenance decreases with animals' growth rate, while the proportion retained is maintained or even increased (Figure 3b). This lower proportion of the protein addressed for maintenance would explain why animals with a higher protein intake would allocate a greater protein proportion for retention, improving the FCR. In the case of the R line rabbits, selected for food efficiency for so many generations (Baselga, 2004), they showed an FCR even better than expected from the relative proportions described above. However, as a consequence of the lower retention of protein as the growth rate of these animals increases, although the remaining amino acids are addressed to body fat deposition, this process is much less effective, avoiding an improvement in the FCR as the growth rate increases within line R (dotted line in Figure 1). Some previous works (Costa et al., 2004; Quevedo et al., 2006) have already observed that the response to the selection for feed efficiency in line R was lower than expected. These results could corroborate the hypothesis of a possible existence of a limiting amino acid that could be affecting the expression of the genetic potential of high growth rate rabbits in the paternal lines. In fact, the clear decrease in the proportion used for maintenance as growth rate increases is not completely compensated by the proportion of protein retained in the body (Figure 3b), slightly increasing the protein not used for any function (neither retained nor used for maintenance). A priori, this result is not expected. The amount of PD ingested that is not used should be lower in animals with higher growth rates, as they generally have a lower protein turn-over and better protein acquisition (McDonald et al., 2010). However, the possible presence of a limiting amino acid in high growth rate animals and the utilisation of the remaining amino acids as a source of energy (less efficient; D'Mello, 1994) could be below this result.

Conclusions

From the results of this work, we can conclude that animals with a high growth rate (as a consequence of genetic selection for this trait) linearly increased their ability to obtain protein from the diet, but they are not more efficient in the digestive used of this protein. Although the amount of protein retained in the body increases with the growth rate of the animals, it is lower than that expected from 50 g/d of average daily gain when moderate protein diets are used, increasing the amount of the protein used for fat accretion, and affecting the genetic progress in feed conversion ratio of these animals. The most plausible reason is the existence of some limiting amino acid when such diets are used in animals with high growth rates. For this reason, determining limiting amino acids requirements during the growing period depending on growth rate could be necessary to allow adequate expression of the genetic potential of animals in the paternal lines, and the proper development of the genetic rankings.

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