Genetics of growth, carcass and meat quality in rabbits

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Abstract

This paper reviews the current knowledge on the genetics of growth, carcass and meat traits in rabbits. There is a great variety in size of rabbit breeds, from which commercial production uses medium size breeds for does and large breeds as terminal sires. Selection experiments for growth and feed efficiency have been successful. Selection for residual feed intake did not modify growth rate, acting on reducing the appetite. Selection for growth rate increased adult weight and led to poorer carcass yield when comparing selected and unselected animals at the same commercial weight, but not at the same age, near the same maturity stage. The results on meat/bone ratio do not show a clear pattern. Negative effects on intramuscular fat and some sensorial traits have been found in lines selected for growth rate, but meat quality in general does not seem to be affected.

Keywords: Rabbit; genetic parameters; growth traits; carcass traits; meat quality; selection

1. Introduction

Growth is decisively important in rabbit meat production. Profit functions and economic weights of rabbit meat production have been estimated by Armero & Blasco (1992), Prayaga & Eady (2000) and Cartuche, Pascual, Gómez, & Blasco (2014). Table 1 shows the costs of a typical industrial rabbitry that can be managed by one person. The main economically important traits in rabbit meat production are feed conversion rate (FCR) and litter size. This means that feed efficiency (measured as FCR, feed intake or residual feed intake) can have a decisive influence on profits. Feed conversion rate is difficult and expensive to measure, so correlated traits, such as growth rate, are often used in selection programmes with the aim of improving FCR indirectly, although genetic correlations are not as favourable as in other species. Selection programmes in rabbit commercial schemes are based on three way crosses, in which two lines are selected for litter size and crossed to produce a crossbred commercial doe, and one line is selected for average daily gain (ADG) in order to produce terminal sires (Baselga & Blasco, 1989; Lebas, Coudert, Rochambeau, & Thébault, 1997). This scheme is similar to what is currently used in swine. However, there are important differences, as some aspects of meat quality (e.g., PSE: Pale, Soft, Exudative meat) play an important role in swine schemes and not in rabbits, which do not present PSE meat. Moreover, selection for reducing fat content is important in pigs, but as rabbits have very lean carcasses when sold (Dalle Zotte, 2002; Hernández & Gondret, 2006), fat content is not an important trait.

Table 1 Distribution of the costs of an industrial rabbitry with 750 reproductive does. Management in batches with A.I. Weaning at 35 days and slaughter at 2.2 kg of live weight (63 days). Elaborated from Cartuche *et al.* (2014).

	€ / doe year	€ / kg live weight	% total
Feeding rabbits for slaughter	60.5	0.53	29.4
Feeding does	32.7	0.28	15.9
Artificial insemination	8.69	0.08	4.2
Replacement reproductive stock	11.8	0.10	5.7
Health	14.3	0.12	6.9
Labour	37.3	0.32	18.1
Amortisation	20.2	0.18	9.8
Others	20.7	0.19	10.1

An important issue when comparing rabbit breeds or lines is to do the comparison at the same stage of maturity. Comparisons at the same commercial weight but a different stage of maturity can be interesting for commercial reasons, but not for finding genetic differences between groups related to carcass or meat quality. As some lines grow quicker than others do, when comparing animals at the same LW or carcass weight, rabbits of some lines are slaughtered at earlier ages, they are younger and the characteristics of the meat are different for two reasons: one is the genetic difference between lines and the other is the differences due to the age. Both effects are confounded, thus if the interest is in genetic differences between lines, they should be compared at the same stage of maturity; i.e., at the same proportion of adult body weight (BW) (Taylor, 1985). Many differences found between breeds or groups of animals under different treatments disappear or are substantially reduced when compared at the same stage of maturity. In commercial rabbit lines, if adult weight is not available, Pascual, Calle & Blasco (2015) showed that comparisons at the same age can be used as a good approximation, but caution should be taken when comparing lines of very different size at the same age, because even at the same age, the stage of maturity can also be different (Ouhayoun & Rouvier, 1973).

2. Genetics of growth traits

2.1. *Between-breed genetic variability*

Rabbits show a great variation in breed size, from dwarf (about 1 kg of adult weight) to giant lines (about 7 kg of adult weight). From the large variety of existing breeds of rabbits, commercial production uses medium size breeds for reproduction due to their high prolificacy, and large breeds as terminal sires due to their high growth rate. This also facilitates doe management and lowers the maintenance cost, allowing the production of commercial rabbits with a high growth rate.

Comparisons between breeds of very different size have not been published in standard refereed journals but are available in proceedings of congresses by Ouhayoun & Poujardieu (1978) and by Bolet, Brun, Monnerot, Abeni, Arnal, Arnold,… & Zimmermann (2000). Large differences in ADG (more than 15 g/d between 4 wk and 11 wk of age were found between breeds, as expected. An interesting result is the between-breeds negative (favourable) relationship between FCR and growth rate found by Ouhayoun & Poujardieu

(1978). FCR between 4 wk and 11 wk varied from 3.61 of Flemish Giant to 4.52 of Small Russian. This type of results has been explained by McCarthy (1980) as due to a better thermoregulation per kg of live weight (LW) of heavy breeds; maintenance energy is lower per kg of BW in giant lines because it is proportional to metabolic weight, which is a power of BW lower than one ($BW^{0.75}$ in the case of adult BW. Therefore, more energy is available for growth in giant lines.

2.2. *Genetic parameters of growth traits*

There are many estimates of heritabilities of weight at a given age, typically at slaughter time (SW), which varies between countries from 9 wk (Spain) to 13 wk of age (North of Italy). There are also many heritability estimates of weaning weight (WW), daily gain (SW-WW) and ADG. Hernández & Gondret (2006) give an average heritability for SW of 0.27 from 17 publications, ranging from 0.12 to 0.67. Although they are widely used, average estimates of many papers are not very useful for several reasons. First, estimates may differ in quality, as some have large standard errors or are biased due to the model used or the method of estimation. Second, environmental variability can differ among farms. Third, negative estimates are not normally published or methods of estimation force estimates to be positive, producing bias in the average of estimates. Fourth, some relationships used may lead to estimates that contain non-additive variability (for example, dominance, epistasis, maternal effects, etc.). Generally speaking, estimates of heritabilities tend to be optimistic, so it is usually better to examine the estimates from selection experiments in which control populations or divergent selected populations can offer additional evidence provided by realised heritability estimates. Recently, Piles, David, Ramon, Canario, Rafel, Pascual, Ragab & Sánchez (2017) have shown that selecting rabbits for daily gain under *ad libitum* conditions can be inefficient under restricted feeding, due to competition between rabbits for feed under restricted conditions. This should be taken into account when selecting for commercial rabbit farms, if they keep their rabbits under a restricted feeding regime.

Estimates of genetic correlation between growth rate and FCR are lower than those found in other species. Although they have a wide confidence interval, the three values available in the literature are quite similar; Piles, Gómez, Rafel, Ramon & Blasco (2004) give -0.49 (confidence interval at 95% probability [-0.94. -0.10]) and -0.47 (confidence interval at 95% probability [-0.99, 0.13]) for two different populations, and Drouilhet, Gilbert, Balmisse, Ruesche, Tircazes, Larzul & Garreau (2013) give -0.38 (s.e. 0.18, which leads to an approximate confidence interval of [-0.74, -0.02]). As the heritability of FCR is not different from the heritability of ADG (between 0.22 and 0.31; Piles *et al.* (2004), Drouhillet *et al.* (2013)), if the true genetic correlation is around -0.4 or -0.5, selection for growth rate would be considerably less efficient for improving FCR than direct selection for FCR.

Measures of feed efficiency other than FCR have been proposed and we discuss them in paragraph 5.2. Proposed by Koch, Swiger, Chambers & Gregory (1963), residual feed intake (RFI) is the difference between actual feed intake and expected feed intake, according to the requirements for maintenance and growth of the animal. Residual feed intake is often estimated as the residual of a regression equation of feed intake (FI) on ADG and average metabolic weight (average LW between 30 and 63 d to the power 0.75). Residual feed intake has a low heritability (0.10 to 0.16) according to results of Drouilhet et al. (2013). The high value (0.45) from Larzul & Rochambeau (2005) comes from a short divergent selection experiment (one generation) in which growth estimates of BW, ADG and RFI were all unusually high, thus their results should be taken with caution. Genetic correlation between RFI and FCR is very high (0.96, s.e. 0.03, Drouilhet *et al.* 2013) which means that both traits probably have a similar genetic basis. If this is the case, as the heritability of FCR is much higher, the advantage of using RFI instead of FCR in selection is unclear. Piles, García-Tomas, Rafel, Ramon, Ibañez-Escriche & Varona (2007) have estimated heritabilities of the partial regression coefficients used to define RFI using Bayesian techniques (Blasco 2017). Estimates of the heritability of these coefficients are similar to the estimates for ADG. In paragraph 3.2, we shall discuss advantages and drawbacks of the different forms of measuring feed efficiency.

3. Genetics of carcass traits

3.1. *Between-breed genetic variability*

Comparisons of different breeds and crosses show different tendencies when performed at the same age (Brun & Ouhayoun, 1989, 1994; Lukefahr, Hohenboken, Cheeke, Patton & Kennick, 1982; Metzger, Odermatt, Szendrő, Mohaupt, Romvári, Makai, … & Horn 2006a; Metzger, Odermatt, Szendrő, Mohaupt, Romvári, Makai, … & Sipos, 2006b;

Ouyed, Rivest & Brun, 2011; Ozimba & Lukefahr, 1991; Szendrő, Matics, Gerencsér, Radnai, Lengyel, Nagy, Riovanto & Dalle Zotte, 2009; Szendrő, Matics, Gerencsér, Nagy, Lengyel, Horn & Dalle Zotte 2010; Rouvier, 1970) or at the same BW (Gómez, Baselga, Rafel & Ramon, 1998; Hernández, Ariño, Grimal & Blasco, 2006; Pla, Hernández & Blasco, 1996; Pla, Guerrero, Guardia, Olivier & Blasco, 1998).

Breeds with a lower adult BW consequently have a higher maturity at slaughter, as observed by Gómez *et al.* (1998) Hernández *et al.* (2006) and Pla et al.1 996, 1998). They had better dress out percentage, lower ratio of the fore part, higher ratio of the hind part and greater fat depots (e.g. perirenal fat weight).

The number of studies evaluating the effects of heterosis based on the different crosses is scarce (Brun & Ouhayoun 1989, 1994; Ouyed *et al.* 2011). Although in some cases favourable results were obtained for carcass yield and carcass fatness, carcass composition traits were generally unaffected by individual or by maternal heterosis.

3.2. ***Genetic parameters of carcass traits***

Due to the large samples needed to estimate genetic parameters with enough precision, the number of studies estimating the genetic parameters for carcass traits of rabbits is scarce. Heritability estimates of the weight of different carcass parts are in general moderate, and common litter effects are also moderate (Al-Saef, Khalil, Al-Dobaib, Al-Homidan, García & Baselga, 2008; Ferraz, Johnson & Eler, 1991; Ferraz, Johnson & Van Vleck, 1992), (ranging between 0.29 and 0.39), but they are equal or higher than the respective heritabilities of the body parts showing maternal influence for these traits. The heritability estimates of carcass ratio traits have been generally higher than those for carcass parts and carcass composition traits, and varied from moderate to high. The highest heritability estimate was observed for fat (perirenal fat percentage), whereas muscle percentage, which has much greater importance for consumers, is only moderately heritable. Thigh muscle volume measured in vivo by Computer Tomography (CT) showed low heritabilities (Gyovai, Nagy, Gerencsér, Metzger, Radnai & Szendrő, 2008; Gyovai, Nagy, Gerencsér, Matics, Radnai, Donkó, ... & Szendrő, 2012; Nagy, Gyovai, Radnai, Matics, Gerencsér, Donkó & Szendrő, 2010; Nagy, Gyovai, Radnai, Nagyné Kiszlinger, Farkas & Szendrő, 2013), but the average surface of the CT estimation of *Longissimus dorsi et lumborum* (LTL) muscle had a substantially higher heritability. Using ultrasound, the heritability of

Longissimus lumborum muscle surface (between the 2nd and 3rd lumbar vertebrae) was moderate (Lenoir & Morien, 2015, 2016). The magnitude of maternal effects was generally low for carcass components (Krogmeier, Dzapo & Mao, 1994) and for muscle traits measured in vivo (Gyovai *et al.* 2008, 2012; Nagy *et al.* 2010, 2013).

Dress out percentage has a moderate heritability, according to a large number of studies. However, dress out percentages of the different studies were not directly comparable, as slaughter time was different (96 vs. 63 days) (e.g. Krogmeier *et al.* 1994 vs. Garreau, Eady, Hurtaud & Legarra, 2008; Larzul, Gondret, Combes & de Rochambeau, 2005), some studies did not follow the WRSA recommendations (Blasco, Ouhayoun & Masoero, 1993; Blasco & Ouhayoun, 1996) for dissection, distal parts of the legs were not removed (Rouvier 1970) or carcasses did not include the head (Ferraz *et al.* 1992; Lukefahr, Odi & Atakora, 1996). Moreover, several authors (Al-Saef *et al.* 2008; Ferraz *et al.* 1992; Krogmeier *et al.* 1994) used hot carcass weight for calculating dress out percentage instead of cold carcass weight. There is only one experiment reporting different heritabilities for different colour values, ranging from 0.11 of b* (yellowness) to 0.36 of a* (redness) (Martínez-Álvaro, Hernández & Blasco A. 2016a).

Sample size of carcass studies is limited due to its cost. As large samples are needed to estimate genetic correlations with precision, estimates of the published experiments have large standard errors and should be taken with caution. The available literature is limited to only a few publications. Garreau *et al.* (2008) and Krogmeier *et al.* (1994) did not find a genetic correlation between dress out percentage and perirenal fat percentage. Nagy, Ibañez, Mekkawy, Metzger, Horn & Szendrő (2006) have published some genetic correlations based on CT scans, observing a negative genetic correlation between muscle LTL volume and perirenal fat weight and a moderately high genetic correlation between the average cross sectional area of the LTL muscle and dress out percentage. This latter finding was corroborated by Lenoir & Morien (2015) using ultrasound technique. Thigh muscle volume showed a null genetic correlation with dress out percentage and a moderately strong correlation with hind part percentage (Nagy *et al.*, 2010). Consequently, selection for thigh muscle volume by CT might also improve hind part percentage.

4. Genetics of rabbit meat quality

Meat quality depends on many traits affected by different metabolic pathways. Hitherto no single genes affecting rabbit meat quality have been discovered, thus the genetic determination of meat quality in rabbits is multi-trait and seemingly multifactorial. Meat quality is measured after slaughter and the traits measured are often difficult and expensive to record. These difficulties, plus the fact of having neither a single measure nor a single gene to concentrate the efforts to improve meat quality, prevent the inclusion of meat quality in selection programmes. Nevertheless, the consequences on meat quality of current selection programmes for growth should be examined.

4.1. *Genetic variability between rabbit lines*

Differences between lines or crosses have been found for several meat traits. These differences may be due to differences in the genetic composition of the lines compared. However, in meat quality studies, the sample size is small because traits are difficult and expensive to record, which often leads to non-significant differences that could be relevant. For example, small sample sizes sometimes do not allow us to draw conclusions when comparing lines. For both reasons, variability in the genetic composition of the lines compared and small sample size, the comparison between lines is not very informative and often helps only as a first indication about the variability that can be found for certain characteristics. Given the great variability in size among rabbit lines, some studies have associated differences in some meat characteristics to differences in line size. Hulot & Ouhayoun (1999) reviewed the literature on breed differences in meat pH, finding substantial differences between lines or crosses (roughly one standard deviation of the trait). In general, no association between breed size and meat pH can be inferred, as no clear pattern appears. Blasco & Piles (1990) did not find any correlation within lines between carcass weight and meat pH.

Differences in meat colour values (L*a*b*) have also been found by Bernardini Battaglini, Castellini & Lattaioli (1995), Hernández *et al.* (2006) and Dalle Zotte, Szendrő, Gerencsér, Szendrő, Cullere, Odermatt, …, & Matics (2015) in lines of different sizes, but without a clear pattern either. No differences in water holding capacity (WHC) were found by Bernardini Battaglini *et al.* (1995) and Ariño, Hernández & Blasco (2006) when comparing lines of different size.

Differences in meat texture between synthetic giant and medium lines were reported by Lukefahr *et al.* (1982) and by Ariño *et al.* (2006). In both cases, the heavy lines were more tender, and in the study of Ariño *et al.* (2006), the heavier line had higher proteolytic activity and lower collagen content. Ariño, Hernández, Pla & Blasco (2007) also performed a sensory analysis, finding differences in tenderness in the same direction, but no differences in flavour or odour traits were found.

Using the same lines, Ramírez, Díaz, Pla, Gil, Blasco & Oliver (2005) and Hernández, Cesari & Blasco (2008) compared lipid content and fatty acid composition of rabbit hind leg meat and perirenal fat. They found no differences in MUFA, but lower SFA and higher PUFA percentages in one of the lines selected for litter size; the differences were substantial, more than one standard deviation of the indices. Other authors (Gasperlin, Polak, Rajar, Skvarea & Lender, 2006) found no differences in SFA, MUFA and PUFA between a local breed and a commercial breed, but their experiment had a small number of animals and s.e. were high. Hernández *et al.* (2008) also found differences in lipolytic activities between a line selected for growth rate and lines selected for litter size, but free FA after refrigerated storage were not influenced by rabbit line. No differences were found either for the enzyme activity of the muscle energy metabolism, such as aldolase and ICDH, or for oxidative parameters (Hernández et al. 2006).

4.2. *Genetic parameters of meat quality traits in rabbits*

The only meat quality traits for which reliable estimates of heritability have been published are muscular pH, colour, intramuscular fat, meat FA profile and instrumental texture. Larzul *et al.* (2005) gave a heritability estimate of 0.16 for ultimate pH (pHu), but its s.e. was high (0.09) and it was not different from zero. A similar result, 0.08 with a 95% confidence interval of [0.01, 0.20] was found by Martinez-Alvaro *et al.* (2016a). However, Larzul & Rochambeau (2005) gave a heritability of 0.50 (s.e. 0.16); despite its large confidence interval, this result suggests that selection might be possible on pHu. Carcass colour (L*a*b*) shows conflicting results, with heritabilities near zero (Larzul & Rochambeau, 2005; Larzul *et al.* 2005), or between 0.14 and 0.25 (Martinez-Alvaro *et al.* 2016a). The latter result is consistent with the correlated response to selection found in an experiment by Hernández, Aliaga, Pla & Blasco (2004) that we shall see in paragraph 5.3. A Bayesian estimate of heritability (Blasco 2017) of intramuscular fat (IMF) was provided by Martinez-Alvaro *et al.* (2016a). The estimate was 0.54, with a probability of 95% of being higher than 0.40, and this high heritability was corroborated by results of a selection experiment, as we shall see later. Genetic correlations between IMF and carcass fat depots were positive but relatively low (0.3), of the same order as the correlation between IMF and reference carcass weight, meat/bone ratio and pHu (Martinez-Alvaro *et al.* 2016a). This is an interesting result, showing that an increment in meat quality increasing IMF is not necessarily accompanied by a rapid impairment of carcass quality incrementing fat depots. A single study estimating heritabilities of fat composition (Martinez-Alvaro *et al.* 2016a) shows low heritability (0.09) for SFA, and high heritabilities for MUFA (0.61) and PUFA (0.45), as well as for the PUFA:SFA ratio (0.42). Genetic correlations between IMF and meat FA percentages were strong and positive for MUFA, with a strong and negative PUFA and PUFA:SFA ratio. Correlation between IMF and SFA was positive, but the estimate had a wide confidence interval. Martinez-Alvaro *et al.* (2018c) also found high heritabilities for percentages of individual FA C14:0, C18:0, C16:1, C18:1n-9, C18:2n-6 and C20:4n-6. High positive genetic correlations were found between IMF and C14:0, C16:1, C18:1n-9 and strong negative correlations for C18:0, C18:2n-6, and C20:4n-6. All these estimates were corroborated by observed correlated responses to selection, described in section 5.5. Instrumental texture (Warner-Bratzler shear force; WBSF) showed a high heritability, 0.57 (Larzul *et al.* 2005), with a rather surprising low s.e. (0.02). Genetic correlations between growth rate and pHu, and growth rate and WBSF, were not different from zero. The former correlation agrees with the null correlated response in pH obtained in selection experiments for growth rate, but the correlation between WBSF and growth rate was not confirmed by selection experiments, as described in paragraph 5.3.

5. Selection experiments

A common problem when evaluating selection experiments is the lack of a control population for estimating the response to selection. When a control is not available, mixed model techniques allow us to estimate this response, but the estimate is heavily dependent on the estimates of genetic parameters used in the model. If these parameters are estimated with the same set of data or in the same population, a better estimate of the response is obtained. However, experience shows that heritabilities are often overestimated due to biases from ignoring non-additive variability or part of the environmental variance. For example, it is well known that the litter size estimates of heritabilities are around 0.10 and that the responses of selection experiments are much lower than expected. Divergent selection experiments allow us to use each population as control of the other, but symmetry in the response is not guaranteed and, consequently, biased estimates of response may result. A control population gives a set of data not affected by selection and provides the means to obtain an unbiased estimate of response although, due to limitations in experimental facilities, it is less accurate than those obtained using mixed model methodology. We consider selection experiments for growth, feed efficiency and meat quality in this review.

5.1. ***Selection for growth***

Only published experiments on selection for growth rate are hereafter considered, whereas multipurpose lines or lines selected for other traits are not contemplated. Responses to selection for growth rate have been reported by Rochambeau, de la Fuente, Rouvier & Ouhayoun (1989), Lukefahr *et al.* (1996), Piles & Blasco (2003) and Larzul *et al.* (2005) with a control population, and two divergent selection experiments were performed by Moura, Kaps, Vogt & Lamberson (1997). Recently, an experiment of selection for ADG under restricted feed consumption was carried out by Drouilhet *et al.* (2013) and Drouilhet, Achard, Zemb, Molette, Gidenne, Larzul, … & Gilbert (2016), as nowadays in intensive farming conditions the rabbits are generally under restricted feeding regimes to prevent digestive disorders after weaning. Other studies have a less clear interpretation (Rochambeau, Retailleau, Poivey & Allain, 1994; Ferraz *et al.* 1992), or an arguable methodology (Niedzwiadek, Fijal & Bielanski, 1992).

In all these experiments, the selection was successful. In those with a control population, Rochambeau et al. (1989), selecting for ADG between 30 and 77 days of age, obtained a response per generation of 0.83 g/d in eight generations of selection, which represents a progress of 2% of the mean per generation. Piles & Blasco (2003) obtained lesser progress, 0.56 g/d per generation in seven generations of selection, 1.2 % of their mean per generation. In both experiments a correlated response was observed in slaughter weight (SW) (77 and 63 days of age, respectively), but not in weaning weight (WW). This is expected, as weight gain after weaning is a large part of SW. Lukefahr *et al.* (1996) directly selected by LW at 70 days, obtaining a correlated response in five generations of selection of 2.7 g/d from 28 to 70 days of age, which represents 1.4% of the mean per generation. Larzul *et al.* (2005) selected for LW at 63 days in a divergent selection experiment, also with a control population. The difference between high and low lines for ADG between 28 and 63 days of age after five generations of selection was 12 g/d, the control population being intermediate between both values. As response was symmetrical, the correlated response per generation in ADG was 6 g/d in five generations, 1.2% per generation. The divergent selection experiment for ADG of Moura *et al.* (1997) gives a difference between high and low line of 8.4 g/d from 56-60 days to 84-88 days of age, which means 4.5% of the mean per generation, or 2.25% per generation if the response was symmetrical. However, it appears that Moura *et al.* (1997) had greater success in decreasing daily gain than in increasing it. Under restricted feeding, selection for ADG led to a response of 1.9 g/day after nine generations of selection, corresponding to 0.5% of the mean of this trait per generation (Garreau, Gilbert, Molette, Larzul, Balmisse, Ruesche, … & Drouilhet, 2015a; Garreau, Gilbert, Molette, Larzul, Balmisse, Ruesche & Secula-Tircazes, 2016), lower than the response found in experiments without restriction. This was expected, as the full potential for growth is not necessarily expressed under restriction. Restricted feeding had an important effect on ADG, and the authors found a difference of 11.2 g/d between restricted and *ad libitum* feeding in their lines.

It is important to note that observed responses were in all cases lower than the expected responses based on previous heritability estimates of ADG or LW. However, as rabbit generation interval for growth rate selection can be very small (six months), the responses would be between 2 and 4% of the mean per year, which are good results compared with other domestic species (Smith, 1984).

5.2. *Selection for feed efficiency*

Several traits measuring feed efficiency can be found in the literature. The most common one is FCR, the ratio between feed intake (FI) and body weight gain (BWG) in a fixed range of days. Recently, RFI has been widely used in several animal species. Both measurements have advantages and disadvantages. A good FCR can be obtained by reducing FI at a given weight, or augmenting LW for a given amount of FI. Selection for FCR acts mainly on the most variable trait, the numerator, and tends to reduce consumption without increasing BWT. This has been observed in growing pigs (see review by Webb 1989), and later in sows (see review by Prunier, Heinonen & Quesnel, 2010), which may create some problems in the future when nutrition demands for maintaining higher litter size will increase. Another issue is that the correlation between FCR and LW or ADG gives rise to the so-called “spurious correlations” (Pearson, 1897), as FCR includes LW in the denominator. Whereas this can be taken into account for interpreting results, it is irrelevant for its inclusion in a selection index, in which correlations are considered to obtain the maximum profit, independently of how they are generated. On the other hand, RFI has also received criticisms. As Kennedy, Van der Werf & Meuwissen (1993) demonstrated, using RFI in a selection index instead of FCR does not add any new information to the index. If RFI is directly selected without its inclusion in an index, profits will be lower, as the component traits are not weighted to obtain the maximum benefit, as the index does. Besides, we have seen before that RFI in the rabbit seems to have a genetic correlation with FCR close to one but a lower heritability, so its use in selection would be less efficient for improving feed efficiency than measuring FCR directly. Moreover, RFI is not a residual, but an estimate of a residual; this means that the error of estimation and the correlations between estimated residuals are not considered (residuals are uncorrelated, but the estimates of residuals are not). A further criticism is that metabolic weight, when used in the definition of RFI, is estimated as BW to the power of 0.75, which is right for adult animals, but metabolic weight in growing animals can have quite different powers, being about 1.0 –i.e., directly proportional to weight─ during growth (Brody 1945, pp. 448-449; Taylor 2009). Selection index for ADG and FI or FCR using appropriate economic weights should be the method giving the highest expected profit. However, selection indexes are sensitive to errors in the estimation of genetic parameters, which can lead to lower profits than expected. If so, selection for FCR or RFI may produce better results.

Experiments on feed efficiency in rabbits have been performed selecting for FCR (Moura *et al.* 1997), RFI (Larzul & Rochambeau, 2005; Drouhillet *et al.* 2013, 2016) and ADG under restricted feeding (Drouillet *et al.* 2013, 2016). The divergent selection experiment of Moura *et al.* (1997) reports inconsistent results for the differences between lines, with the high line having a lower FCR than the low line at the end of the experiment. However, using mixed model techniques they found a symmetric progress of 0.6% per generation in each direction for FCR in the period ranging from 56-60 days to 84-88 days of age. The divergent selection experiment on RFI carried out by Larzul & Rochambeau (2005) was too short to drive conclusions; they only had one generation of selection and their results comparing high and low lines were not significant, therefore nothing can be said about whether selection on RFI was successful or not. A longer experiment was carried out on RFI between 30 and 65 d of age by Drouilhet *et al.* (2013, 2016), showing remarkably similar results when using a control population or analysing the whole experiment by using mixed model techniques. After nine generations of selection, they found a response of -39 g of RFI per generation, and a correlated response of -0.20 in FCR, corresponding to decreases of 0.9% and 0.8% per generation, respectively (Garreau *et al.* 2015a, 2016). No correlated response was found for growth rate, showing that selection acted upon reducing appetite.

5.3. *Consequences of selection for growth rate or feed efficiency*

Selection experiments have been successful, and the cumulative progress per year allows us to increase growth rate substantially in a few years' time. This has several consequences, which we shall subsequently examine:

5.3.1. *Changes in adult weight*

As Taylor (1985) stressed, all BW are genetically correlated and selection for growth rate should lead to an increase in adult weight. This was shown in rabbits by Blasco *et al.* (2003) fitting growth curves to a line selected by growth rate and to a control population. Adult weight increased by 1% per generation, near the progress obtained in growth rate. Taylor (1980) suggested comparing growth curves by representing them in a metabolic scale in which the axes would be stage of maturity (i.e., weight divided by adult weight) from 0 to 100%, and metabolic time. This metabolic time comes from the observation by Taylor (1965) that time to reach maturity is proportional to metabolic adult weight (Taylor estimates metabolic adult weight as adult weight to the power of 0.73), thus 'metabolic time' is actual time divided by metabolic adult weight. When curves of the selected and control populations were represented in Taylor's metabolic scale, the effect of selection disappeared, showing that selection did not change the shape of the curve (Blasco, Piles & Varona, 2003) and that adult weight increased due to a scale effect. In consequence, lines selected for growth rate would become giant lines, more expensive to maintain and manage. Nevertheless, in modern industrial rabbit production this should not be a serious problem, as artificial insemination is widely used and very few terminal sires are needed.

5.3.2. *Changes in FCR*

As SW is determined by the market, lines selected for growth rate are slaughtered at earlier ages, saving on feeding costs. This is the main cause of the improvement in FCR. When compared at the same age, the selected line will have a higher LW and consequently a better use of energy for maintenance, as the losses are proportional to a power of BW lower than 1 (0.75 for adult weight). Larzul *et al.* (2005) did not find differences in FCR between a line selected for ADG and the control line after five generations of selection. The only direct evidence of FCR improvement through selection on ADG comes from the three generations of the selection experiment of Moura *et al.* (1997), showing consistently lower values for FCR in the line selected to increase ADG, and a progress around 3.5% of the mean of the trait per generation in each direction. However, the line selected for FCR did not show appreciable changes in ADG, so no straightforward conclusions can be drawn from the experiment. Consequences of selection for growth rate on feed efficiency can also be drawn from estimated genetic parameters. Unfortunately, many data items (at least a few thousand) are needed to estimate genetic correlations with reasonable accuracy, and this is not feasible for traits like individual FCR that are expensive to measure. Under restricted feeding, Garreau, Molette, Gilbert, Larzul & Balmisse (2015b) found a correlated response in FCR of -0.19, corresponding to 0.8% of the mean per generation, a remarkably similar result to the response for FCR in their line selected for RFI quoted previously (Garreau *et al.* 2015a). As the crucial trait in rabbit meat production is FCR (Cartuche *et al.* 2014) and both lines had almost the same response to selection for this trait, selection for growth rate under restricted feeding seems easier to implement in a genetic programme. This will produce heavier animals in the long term (Garreau *et al.* 2015a, Drouilhet *et al.* 2016) but if the commercial slaughter weight remains the same, the only consequence would be that rabbits will be slaughtered earlier.

5.3.3. *Changes in carcass quality*

Rabbits selected for growth rate are slaughtered at the same commercial weight as unselected rabbits, thus they are slaughtered at earlier ages and are younger than rabbits that were not selected for growth rate. Slaughtering younger animals implies a poorer carcass yield, a slightly higher bone ratio and a slightly different proportion of retail cuts. A lower fat content is also expected, as fat is a tissue of late deposition; however, selection for growth rate increases appetite, and it is well known in other species that an increment of daily FI can lead to fat deposition independently of age (Whittemore, 1987). The effect of selection for growth rate at fixed BW has been estimated by Gondret, Larzul, Combes & de Rochambeau H (2005) and Pascual & Pla (2007). Both studies found a higher dissectible fat percentage of the carcass and a lower meat/bone ratio in the hind leg of the line selected for increased ADG, and Gondret *et al.* (2005) found a poorer carcass yield in this line, as expected. As rabbits were slaughtered at a different maturity stage, there is confounding between the actual effect of selection and the effect of maturity.

Because retail cuts and tissue composition are highly correlated to BW, large differences are not expected when comparing at the same stage of maturity, as growth curves are almost coincident when they are expressed in metabolic scale. Pascual, Pla & Blasco (2008) have examined the effect of selection for growth rate on the relative growth of carcass tissues and retail cuts. They compared allometric coefficients of retail cuts of the line selected for growth rate by Piles & Blasco (2003) and a control population, and compared hind leg meat and bone tissues. After 11 generations of selection, no effect of selection on the relative growth of any of the components studied was found. The effect of selection for growth rate on carcass composition at the same age has been examined by Lukefahr *et al.* (1996), Hernández *et al.* (2004) and Larzul *et al.* (2005), and by Garreau *et al.* (2015b) under restricted feeding conditions. Lukefahr *et al.* (1996) and Hernández *et al.* (2004) did not find differences between selected and control group in carcass yield, although Larzul *et al.* (2005) found a small difference in favour of the selected line for high ADG. Hernández *et al.* (2004) found less fat in the line selected for ADG than in the control line, a result also found in former analysis of the same line (Piles, Blasco & Pla, 2000), which is not in agreement with results found by Larzul *et al.* (2005), who observed more dissectible fat in the high than in the low line. The norms of the World Rabbit Science Association (Blasco & Ouhayoun, 1996) recommend using the meat and bones of the hind leg for comparisons, as it is more closely related to the meat, bone and meat/bone ratio of the whole carcass. Lukefahr *et al.* (1996) only considered the loin cut, finding no differences between groups, but some advantage for the selected line in muscle/bone ratio of this retail cut. Differences in meat/bone ratio of the hind leg were found by Gondret *et al.* (2005) in their divergent selection experiment for ADG, where the low line had a better ratio than the control, although no differences were found between the control and the high line; conversely, Hernández *et al.* (2004) observed a higher meat/bone ratio in the line selected for ADG. As a general pattern, no differences were found by Hernández *et al.* (2004) between selected and control lines in retail cuts and other parts of the carcass (head, kidneys, liver, lungs and heart). In the study of selection for growth rate under restricted feeding conditions (Drouilhet *et al.* 2013, 2016), a substantial correlated response in perirenal fat was found (19% reduction in 9 generations of selection, 2% of the mean of the trait per generation), although no response in scapular fat occurred. No correlated responses in hind leg, intermediate part of the carcass, meat/bone ratio and carcass yield were found. Their line selected for RFI had an even higher correlated response in perirenal fat (33% in 9 generations of selection, 3.6% of the mean of the trait per generation), and a substantial response in scapular fat (2% of the mean per generation). Favourable correlated responses in hind leg proportion and meat/bone ratio were also obtained in this line.

5.3.4. ***Changes in meat quality***

Changes in meat quality due to selection for growth rate have been investigated by Hernández *et al.* (2004) (study 1), and in a divergent selection experiment by Larzul *et al.* (2005) (study 2), with both experiments using control populations. There are many traits related to meat quality and it is not always easy to summarise them or to find a single way to characterise meat. Among the most important meat quality traits are L*a*b* colour and pHu. Differences in colour between selected and control lines in LTL meat were found in study 1. In rabbits, usually sold as whole carcass or as retail cuts, the colour of the carcass can be considered a quality trait more closely related to consumer preferences than meat quality. Hernández *et al.* (2004) found that the selected line had higher L*, and lower a* and b* values than the control line, whereas in study 2 no differences were observed between selected and control lines. The pHu was measured in the m. LTL in study 1 (Ramírez, Oliver, Pla, Guerrero, Ariño, Blasco, Pascual & Gil 2004) and in m. *Semitendinosus* and m. LTL in study 2 (Larzul *et al.* 2005), and no differences were observed between selected and control lines. As for WHC, it was lower in the selected line of study 1, a difference that was also observed for cooked meat in previous analyses with the same lines, although in cooked meat the evidence was less strong (Piles *et al.*, 2000). There is some evidence in study 1 of selection for growth rate increasing the percentage of fat content in the meat of the hind leg, as well as changes in FA composition. However, changes in indices related to human health were very small, the strongest effect being for the PUFA/SFA ratio, which only decreased from 1.06 to 0.95 in 14 generations of selection (Ramírez *et al.* 2005). Selection for growth rate changed meat toughness in both experiments (study 1: Ramírez *et al.* 2004; study 2: Larzul *et al.* 2005, study 2), but it affected texture parameters without a clear pattern. Nevertheless, no difference in tenderness, juiciness or fibrousness was detected by a trained panel test in study 1. Moreover, muscle fibre analyses, more related to the myofibrillar tenderness, showed no differences in fibre typing and diameter between the line selected for increasing growth rate and the control line (study 2). Selection for growth rate had a negative effect on some sensory traits, as it increased liver flavour and decreased aniseed odour and flavour (study

1; Hernández, Guerrero, Ramírez, Mekkawy, Pla, Ariño, Ibañez & Blasco, 2005). Other traits related to meat quality analyses were also investigated: proteolytic enzyme activities (calpains and cathepsins activities and cysteine proteinase inhibitors) and lipolytic enzyme activities in study 1 showed no effect of selection for growth rate (Gil, Ramírez, Pla, Ariño, Hernández, Pascual, ... & Oliver, 2006). When selecting for growth rate under restricted feeding (see section 5.2), no change of WHC in cooked meat was observed, but some differences in pHu and L* emerged (Molette, Gilbert, Larzul, Balmisse, Ruesche, Manse, … & Drouilhet 2016). Minor unfavourable changes in the latter traits were found for their line selected for RFI.

The general picture is that selection for growth rate does not clearly affect meat quality, with the experiments showing some small changes, not always in the same direction, which may be attributed to genetic drift or sampling error.

5.4. ***Selection for increasing muscle volume***

Based on CT scanning of live rabbits, two divergent selection experiments were performed. In the first experiment (Szendrő, Romvári, Horn, Radnai, Bíró-Németh & Milisits, 1996), male rabbits were selected for the average surface of the m. *Longissimus lumborum* (between the 2nd and 3rd and 4th and 5th lumbar vertebra), and the experiment lasted two and three generations for the low and high lines, respectively. In the second experiment, both males and females were selected (Szendrő, Metzger, Nagy, Szabó, Petrási, Donkó & Horn, 2012), for increasing thigh muscle volume and the trial lasted three generations. The selection experiments were both successful. In the first experiment (Szendrő *et al.* 1996), for the average surface of the m. *Longissimus lumborum* a difference of 1.3 cm^2 was observed between the high and low lines, and a correlated response of 2% for dress out percentage. The intermediate and hind parts of the rabbit carcass differed by 22 and 14 g, respectively, whereas the gastrointestinal tract had a 23 g difference between high and low lines. Similar results were reported in the second experiment (Szendrő *et al.*, 2012), where the difference between the thigh muscle volumes between the high and low lines was 25 cm^3; moreover, the high line had lower FI (128 vs 138 g/d) and better FCR (2.81 vs 3.01). Percentages of the fore part (30.1 vs 29.4%), perirenal fat (2.40 vs 1.90%) and scapular fat (1.07 vs 0.49%) of the reference carcass were higher in the low line, whereas ratios of the hind part (36.3 vs 38.2%) and meat of both hind legs (26.9 vs. 28.7%) were higher in the high line. Therefore, CT-aided selection can improve muscle volume and other carcass traits. The main results of the breeding programme based on CT-aided selection were summarised by Matics, Nagy, Gerencsér, Radnai, Gyovai, Donkó, … & Szendrő (2014).

5.5. *Selection for intramuscular fat content*

Intramuscular fat (IMF) is a main meat quality factor, affecting sensory properties and related to the nutritional value of the meat. A divergent selection experiment on IMF of rabbits was carried out by Zomeño, Hernández & Blasco (2013a, 2013b), Martinez-Alvaro *et al.* (2016a) and Martínez-Álvaro, Penalba, Hernández & Blasco (2016b), evaluating candidates for selection with the IMF of muscle *Longissimus dorsi* from two sibs. After seven generations of divergent selection, they obtained a divergence around 5% of the mean (1.09 g/100 g) per generation, with both lines following a symmetrical trend (Martinez-Alvaro *et al.* 2016a). Positively correlated responses to IMF selection were found in *Biceps femoris*, *Supraspinatus* and *Semimembranosus proprius* muscles (Martínez-Álvaro, Hernández, Agha & Blasco, 2018a). No correlated responses were found for pHu in any muscle. Colour traits of the carcass and of the meat were not affected by selection, (Martinez-Alvaro *et al.* 2016a). Greater lipogenic activities in muscles *Semimembranosus proprius* and LTL, perirenal fat and liver were observed in the high line than in the low line (Martínez-Álvaro, Blasco & Hernández, 2017; Martínez-Álvaro, Paucar, Satué, Blasco & Hernández, 2018b). There was a correlated response in perirenal fat content, which was greater in the high line. Correlated responses were found in meat FA percentages. The low line had greater PUFA and lower MUFA than the high line, whereas SFA was similar in both lines (Martinez-Alvaro *et al.* 2016a), leading to unfavourable values for PUFA/SFA and favourable MUFA/SFA ratios in the high line. In general, individual FA of the MUFA and PUFA groups showed a similar pattern, with the exception of C18:3n-3 percentage, which was greater in the high line. (Martínez-Álvaro *et al.* 2017). The same pattern was found in other muscles (Martínez-Álvaro, Blasco & Hernández, 2018c). The increase of dissectible fat and the worsening in PUFA/SFA ratio means that selection for IMF can deteriorate carcass and meat quality from a nutritional point of view. However, the amount of dissectible fat in rabbit carcasses (2.5% at 9 wk and 3.5% at 13 wk, Hernández *et al.* 2004) and the percentage of IMF are so low in rabbits (about 1%, Zomeño *et al.* 2013a) that differences due to selection would not compromise human health when consuming rabbit meat. Finally, WBSF toughness was 9.9% greater in the low line than in the high line, whereas other instrumental texture and sensory attributes, and cooking loss, were similar in both lines. No effect of selection for IMF was observed in any sensory attributes (Martinez-Alvaro *et al.* 2016b).

6. Conclusion

Rabbit meat is an industrial product in which feed efficiency plays a key economic role. Feed efficiency is indirectly improved by selection on growth rate, although the genetic correlation in rabbit is lower than in other species. Selection for growth rate and feed efficiency has been successful, although feed efficiency selection is restricted to experiments due to the high cost of measuring feed consumption. Selection has consequences in carcass and meat quality, as rabbits are slaughtered at fixed commercial weight, so slaughtering younger animals entails poorer carcass yield, slightly higher bone ratio and slightly different proportions of retail cuts. It seems that it is possible to select for muscle volume by computer tomography, and for some traits related to meat quality such as intramuscular fat but, as with feed efficiency, this selection is difficult to apply at industrial level due to the high cost involved in measuring these traits. Meat quality is not paid for nowadays in rabbit meat markets, and it seems that selection for growth rate is not seriously affecting rabbit meat quality, but it is advisable to monitor changes due to selection for growth rate.

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