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Estimating direct genetic and maternal effects affecting rabbit growth and feed efficiency with a factorial design

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Abstract

The aim of this experiment was to evaluate the significance of neonatal environment on feed efficiency. For that purpose, rabbits from a line selected for residual feed intake (RFI) during 10 generations (G10 kits) were cross-fostered with non-selected control does (i.e., G0 line), and reciprocally. In parallel, sibs were fostered by mothers from their original line. Nine hundred animals were raised in individual ($N = 456$) or collective ($N = 320$) cages. Traits analysed in this study were body weight at 32 days and at 63 days, average daily gain (ADG), feed intake between weaning and 63 days (FI), feed conversion ratio (FCR) and RFI. The maternal environment offered by does from the line selected for RFI deteriorated the FCR of the kits, independently of their line of origin, during fattening ($+0.08 \pm 0.02$) compared to FCR of kits nursed by G0 does. The line, the type of housing and the batch were significant effects for all the measured traits: G10 kits were lighter than their G0 counterparts at 32 days (-82.9 ± 9 g, $p < 0.0001$) and at 63 days (-161 ± 16 g, $p < 0.0001$). They also had a lower ADG (-2.36 ± 0.36 g/day, $p < 0.0001$), RFI (-521 ± 24 g/day, $p < 0.0001$) and a lower FI (-855 ± 31 g, $p < 0.0001$), resulting in a more desirable feed efficiency (FCR: -0.35 ± 0.02). There was no significant difference in the contrast of G10 and G0 performances between collective and individual/digestive cages ($p > 0.22$): −2.35 g/day versus 2.94 g/day for ADG, −0.39 versus −0.40 for FCR, −577 g versus −565 g for RFI and −879 g versus −859 g for FI, respectively). Thus, no genotype-by-environment (housing) interaction is expected at the commercial level, that is, no re-ranking of the animals due to collective housing.

KEYWORDS

feed efficiency, genetics, growth, maternal effect, residual feed intake

1 | INTRODUCTION

Improvement of feed efficiency is essential to increase the competitiveness of the rabbit industry but also to reduce animal excretion and, consequently, decrease the environmental impact of the production. It can be achieved in rabbits by selection on lower residual feed intake (RFI) or on increased growth under restricted feeding (Drouilhet et al., 2013, 2015). However, these selection strategies do not distinguish the direct genetic effect of the animal from the contribution of the maternal environment to the performance, among which the genetic maternal environment and the vertical transmission of the gut microbiota, founding the kit gut microbiota, could contribute significantly. Maternal effects are defined as the *causal* influence of the maternal genotype or phenotype on the offspring phenotype (Wolf & Wade, 2009). It may result

as a consequence of maternal traits, such as nursing (e.g., Gouldsborough, Black, Johnson, & Ashton, 1998), provisioning or licking/grooming of offspring by mothers (e.g., Cameron, Fish, & Meaney, 2008; Cameron, Shahrokh et al., 2008).

To further investigate the effects of the animal genotype and maternal environment on feed efficiency, an experiment based on cross-fostering between a line selected for lower RFI and a non-selected control line was performed, as proposed by Cundiff (1972). The objective of the present study was first to estimate both the host genotype effect and the maternal environment effect on growth and feed efficiency in rabbits, and evaluate how housing in individual or collective cages affects feed efficiency.

2 | MATERIALS AND METHODS

2.1 | Animal management

The experimental rabbit populations were issued from the INRA 1001 line (Larzul & De Rochambeau, 2005) and bred in the experimental INRA farm Pôle d'Expérimentation Cunicole Toulousain (Castanet-Tolosan, France), in accordance with the national regulations for animal care and use of animals in agriculture. Two lines were used in this study: the G10 line selected for 10 generations for decreased RFI (Drouilhet et al., 2013, 2015) and the G0 control line produced from progeny of frozen embryos of the ancestor population of the selected line. The 490 G10 and 410 G0 rabbits were produced in 3 batches with a 42-day interval. Within 48 hr following birth, every kit was fostered; that is, no kit stayed with its biological mother. To avoid microbial transmission, G0 does were placed on one side of the room and G10 does were placed on the opposite side. In each batch, half of the kits were fostered to G0 does and the second half was fostered by G10 does. Does adopted alternatively kits from one line and from the other line in successive batches. Litters of 5 to 7 kits were made up, mixing sires families of kits within fostered litters. Each fostered litter contained either G0 or G10 kits. Sexes could not be identified with certainty at birth so this factor was ignored in the cross-fostering plan.

At weaning (32 days), in each batch, 152 and 48 kits were placed in individual cages and digestibility cages, respectively. The remaining animals were grouped in collective cages containing four to five animals. In total, 456 animals were housed in individual cages, 144 animals in digestibility cages and 320 in collective cages. For individuals housing, the four different groups (rabbit line × foster dam line) were alternated in order to mix as best as possible the place of groups in the room. For collective housing, rabbits were placed in cages according to their group (i.e., G0×G0 in the first cage, G0G10 in the following cage, G10 × G10 in the following cage, G10×G0 in the following cage). The raw means of kit lines by foster doe line is presented in Table 1. All animals were offered feed and water ad libitum, with the same commercial pelleted diet (8.8% crude ash, 14.4% crude protein, 27.9% acid detergent fibre and 9.9% acid detergent lignin, phosphorus 5.31 g/kg, zinc 100 mg/kg, copper 23.8 mg/kg) until the end of the fattening period (63 days).

TABLE 1 Averages of growth and feed efficiency traits by kit line and foster doe line

Doe line	G0		G10	
Kit line	G0 $n = 195$	G10 $n = 229$	G0 $n = 212$	G10 $N = 223$
Trait				
BW32 (g)	925	837	917	834
BW63 (g)	2,647	2,469	2,629	2,436
ADG (g/day)	52.20	49.45	51.88	48.54
FCR	2.98	2.64	3.02	2.71
RFI (g)	235.88	−247.64	296.03	−204.55
FI (g)	5,104.13	4,290.82	5,132.41	4,283.06

2.2 | Traits

Animals were weighed at weaning (BW32) and at 63 days of age (BW63). Total individual feed intake (FI) was recorded in individual and digestibility cages and estimated in collective cages by dividing total feed consumption by the number of animals in the cage. A total of 84 animals died prior to 63 days of age. The total feed consumption was corrected by estimating the feed intake of dead animals. Average daily gain (ADG) was obtained by dividing the body weight gain during the test by the number of days of the growing period (31 days). For animals raised in individual cages, feed conversion ratio (FCR) was calculated as total individual feed intake divided by the body weight gain. For animals raised in collective cages, FCR was calculated as total feed intake of the cage divided by individual body weight gain of each animal of the cage. The feed intake of animals dead before the 63 days weighing was estimated, considering the number of days until death and the average daily feed intake of animals of his cage for this period, and removed in order to obtain the correct total feed intake of weighed animals.

2.3 | Statistical analyses

The RFI was computed as the residual of the multiple linear regression of total individual feed intake on average metabolic body weight (average body weight between weaning and end of the test to the power 0.75) to account for maintenance requirements, and ADG to account for production requirements (REG procedure; SAS software, 2008), as in Drouilhet et al. (2015).

Fixed effects to be accounted for in the statistical analyses were tested applying a linear model and performing a Wald *F* test of the ASReml 4.0 software (Gilmour, Gogel, Cullis, Welham, & Thompson, 2014). A weighted analysis was applied for FI, RFI and FCR. For these traits, data were weighed to take into account the number of recorded animal in each cage at 63 days (1 in individual cages, from 2 to 5 in collective cages).

The linear model is mentioned below:

$$y_{ijklm} = \mu + \text{kit line}_i + \text{doe line}_j + \text{batch}_k + \text{housing}_l + \text{batch}_k \times \text{housing}_l + e_{ijkml}, \quad (1)$$

with y_{ijklm} the trait value for animal k, kit line_i the line of the animal (direct effect, 2 levels), doe line_j the line of the foster doe (maternal effect, 2 levels), batch_k the batch of the animal (3 levels), housing_l, the type of cage in which the animal was raised (3 levels). The type of cage effect was not used in the analysis of BW32. The only significant interaction between all fixed effects was $\text{batch}_k \times \text{housing}_l$ ($p < 0.05$); therefore, no other interaction was retained in the models. Effects were reported as significant when $p < 0.05$.

3 | RESULTS AND DISCUSSION

The kit line, batch and type of housing effects were significant for all traits ($p < 0.001$). The foster doe effect was significant only for FCR ($p = 0.005$). The batch × housing interaction was also significant for all traits.

3.1 | The kit line impacts all the zootechnical measurements

Least square means of the kit line effect are presented in Table 2. The G10 animals were lighter than G0 rabbits at 32 days (−78 ± 9 g), which is in agreement with the unfavourable genetic correlations of RFI with this trait reported by Drouilhet et al. (2013) in the same experimental population (0.85 ± 0.34). The G10 animals were also lighter than G0 rabbits at 63 days (−170 ± 16 g) and had a lower ADG (−2.77 ± 0.36 g/day) which was not in agreement with the previously reported low correlation between RFI and ADG (−0.09 ± 0.20) (Drouilhet et al., 2013). However, Drouilhet et al. (2015) reported much lower final weights in both lines (−540 g in average), reflecting less favourable farming conditions than in our experiment. Therefore, the higher growth observed here in the G0 animals compared to the G10 animals could result from a full expression of their growth potential, allowed by some better farming conditions. RFI selection in pigs shows the same trends, to a lesser extent, with a null or a small correlated response in ADG in two independent RFI selection experiments (Gilbert et al., 2017).

TABLE 2 Least square means of growth and feed efficiency traits in the control line (G0) and the line selected for residual feed intake during 10 generations (G10)

Trait	Kit line		
	G0	G10	*p* value*
BW32 (g)	915 ± 7	837 ± 6	<0.0001
BW63 (g)	2,634 ± 13	2,464 ± 12	<0.0001
ADG (g/day)	52.09 ± 0.28	49.32 ± 0.26	<0.0001
FCR	3.01 ± 0.02	2.66 ± 0.02	<0.0001
RFI (g)	269 ± 17	−252 ± 17	<0.0001
FI (g)	5,107 ± 25	4,252 ± 23	<0.0001

*p value of the line effect in a linear model including the effects of the line of the animal (2 levels), the line of the foster doe (2 levels), the batch of the animal (3 levels), the type of cage in which the animal was raised (3 levels), except for the analysis of BW32, and the interaction between batch and cage effects.

The lower FCR (−0.35 ± 0.02), RFI (−521 ± 24 g) and FI (−855 ± 31 g) of G10 animals illustrated a better feed efficiency. These results demonstrate that selection on RFI resulted in a reduction on the FCR, companied by a decrease of ADG. Thus, the improve on the efficiency in the use of feed shown in this study is less evident than that previously reported by Drouilhet et al. ()2013, 2015. They used a different experimental population from the same line, and in that experiment, the reduction on ADG was null (Drouilhet et al., 2013, 2015). Many similar responses in the reduction on RFI by selection have been reported in pig and poultry (Bordas, Tixier Boichard, & Merat, 1992; Gilbert et al., 2017; Nguyen, McPhee, & Wade, 2005).

3.2 | The foster doe line impacts the feed conversion efficiency

Our results reflect a negative foster doe effect of the selected line G10 on FCR, which is the only trait significantly impacted by the foster doe line. Indeed, G10 foster does had an unfavourable effect on FCR compared to G0 foster does, irrespective of the kit line (+0.08 ± 0.02, $p = 0.005$) (Figure 1). There was no interaction between kit line and foster doe line. Although the difference was not significant, the unfavourable effect of G10 foster doe is partially explained by a lower ADG (50.4 ± 0.2 g/day versus 50.8 ± 0.3 g/day) and a higher FI (4,723 ± 24 g versus 4,712 ± 25 g).

The foster doe effect includes, among others, the milk offered by the doe to the kits, the maternal behaviour and the effect of the gut microbiota transmitted to the kits. At this stage of the study, it is not possible to identify which component of foster doe effect was degraded by the selection (Combes et al., 2013). The unfavourable link between direct and maternal

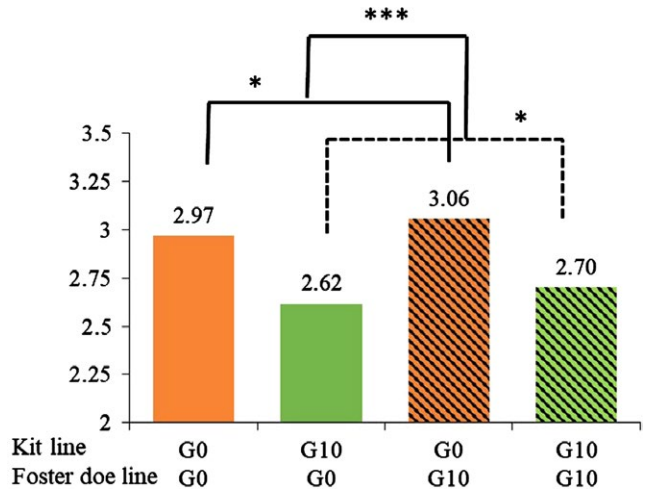

FIGURE 1 Kit line and foster doe line effects on feed conversion ratio. *$p < 0.05$; ***$p < 0.001$

effects echoes to negative correlations previously estimated between direct and maternal effects on production traits in rabbits (David et al., 2015). This negative effect could be due to the selection of traits that are favourable for RFI in fattening at the expenses of maternal qualities, such as milk production after kindling. Lee (2002) reported negative genetic correlations between body weight and milk yield in a review, illustrating genetic antagonism between direct and maternal effects. The genetic correlation between direct and maternal effects of FCR was not significantly different from zero (−0.28 ± 0.33) in the G10 line (Garreau, unpublished). A biological point of view for genetic antagonism between direct and maternal effects in mammals is given by Bauman and Currie (1980): this antagonism could be explained by partitioning of nutrients to various functions (growth, foetus development, lactation…). However, selection for low RFI can favour rapid mobilization of resources to lactation. For example, pig selection for low RFI during growth produced sows with improved performance during lactation, with increased number of piglets and litter growth, increased mobilization of body reserves and lower feed intake (Gilbert et al., 2012; Young, Bergsma, Knol, Patience, & Dekkers, 2016). In addition, favourable relationships between direct and maternal effects of feed efficiency were observed in broiler (Romero, Zuidhof, Renema, Naeima, & Robinson, 2011) and in cattle (Hoque, Arthur, Hiramoto, Gilmour, & Oikawa, 2007).

TABLE 3 Least square means of growth and feed efficiency traits in collective, digestibility and individual cages

	Type of housing*			
Trait	**Collective**	**Digestibility**	**Individual**	***p* value†**
BW63 (g)	2,449 ± 14[a]	2,597 ± 20[b]	2,601 ± 11[b]	<0.0001
ADG (g/day)	48.12 ± 0.30[a]	52.06 ± 0.43[b]	51.92 ± 0.24[b]	<0.0001
FCR	3.05 ± 0.02[a]	2.70 ± 0.02[b]	2.70 ± 0.01[b]	<0.0001
RFI (g)	217 ± 13[a]	−113 ± 27[b]	−139 ± 16[b]	<0.0001
FI (g)	4,646 ± 26	4,653 ± 38	4,639 ± 21	<0.0001

*Different letters indicate least square means differing within row ($p < 0.05$). †p value of the cage effect in a linear model including the effects of the line of the animal (2 levels), the line of the foster doe (2 levels), the batch of the animal (3 levels), the type of cage in which the animal was raised (3 levels), except for the analysis of BW32, and the interaction between batch and cage effects.

TABLE 4 Least square means of growth and feed efficiency traits for kit line by type of housing

Type of housing						
	Collective		**Digestibility**		**Individual**	
	Kit line					
Trait	**G0**	**G10**	**G0**	**G10**	**G0**	**G10**
BW32 (g)	902 ± 12[a]	819 ± 9[b]	910 ± 15[a]	847 ± 15[b]	932 ± 8[a]	844 ± 8[b]
BW63 (g)	2,529 ± 22[a]	2,368 ± 17[b]	2,691 ± 28[a]	2,502 ± 28[b]	2,681 ± 15[a]	2,522 ± 15[b]
ADG (g/day)	49.30 ± 0.48[a]	46.95 ± 0.37[b]	53.97 ± 0.62[a]	50.16 ± 0.62[b]	52.99 ± 0.34[a]	50.84 ± 0.34[b]
FCR	3.30 ± 0.03[a]	2.91 ± 0.02[b]	2.90 ± 0.04[a]	2.50 ± 0.04[b]	2.90 ± 0.02[a]	2.50 ± 0.02[b]
RFI (g)	580 ± 36[a]	3 ± 28[b]	166 ± 46[a]	−392 ± 46[b]	144 ± 25[a]	−428 ± 26[b]
FI (g)	5,200 ± 45[a]	4,321 ± 35[b]	5,079 ± 58[a]	4,228 ± 58[b]	5,069 ± 32[a]	4,202 ± 32[b]

Notes. Different letters indicate least square means differing within row ($p < 0.05$).
Least square means obtained from a linear model including the effects of the line of the animal (2 levels), the line of the foster doe (2 levels), the batch of the animal (3 levels), the type of cage in which the animal was raised (3 levels), except for the analysis of BW32, and the interaction between batch and cage effects.

3.3 | Results apply to collective cages

The results of rabbits in collective cages differ slightly from those obtained on rabbits raised individually (Table 3): rabbits raised in collective cages had higher FCR, RFI (+0.35 ± 0.02, and +205 ± 24 g, respectively, $p < 0.0001$) but FI was the same in both type of housing. They were lighter at 63 days (−162 ± 17 g, $p < 0.0001$) and had a lower ADG (−4.21 ± 0.37 g/day, $p < 0.0001$) than rabbits raised in individual cages. Xiccato, Trocino, Majolini, Tazzoli, and Zuffellato (2013) found similar results for growth comparing 72 rabbits in individual cages with 216 rabbits in collective cages of nine animals: The rabbits housed in individual cages showed higher daily weight gain both during the fattening period (43.0 versus 41.5 g/day; $p < 0.05$), and they had a higher final live weight at 75 days of age (2,678 versus 2,602 g; $p < 0.05$). However, the authors reported higher FI for rabbits raised in individual cages (133 g/day versus 126 g/day; $p < 0.01$), and finally, FCR did not differ significantly among rabbits housed in the two types of cages.

The G10 animals were selected for reduced residual feed intake in individual cages and fed ad libitum. However, despite the trait differences depending on the housing conditions, rabbits from the selected line were more efficient whatever the type of housing, individual or collective. In each type of housing, the kit line effect was significant for all traits (Table 4). The contrast between G10 and G0 kits performance was not significantly affected by housing in collective and in individual/digestive cages ($p > 0.05$): −82 ± 15 g versus −77 ± 10 g for BW32, −161 ± 32 g versus −174 ± 17 g for BW63, −2.35 ± 0.77 g/day versus 2.94 ± 0.33 g/day for ADG, −0.39 ± 0.05 versus −0.40 ± 0.02 for FCR, −577 ± 54 g versus −565 ± 20 g for RFI and −879 ± 56 g versus −859 ± 35 g for FI, respectively. This result shows that selection for feed efficiency is efficient to reduce FCR whatever the type of housing, individual or collective but still highlight the unfavourable response on ADG, lower in G10 kits than in G0 kits whatever the type of housing. It must be reminded that animals were fed ad libitum but there could be an interaction genotype × type of housing with a restricted feeding, which is a common management technique in production farms, especially in France. Altogether, the collective housing, which is commercial typical housing, represents a decrease of ADG by 9% and a 13% increase of FCR compared to individual housing that affects the farms economic results. The main difference between the housing systems is the possibility for animals to have activity and interactions with others. Feed, sanitary conditions and management were exactly similar, and the animals were all housed in the same building. This result is in accordance with previously reported results where less rabbits per cage lead to heavier animals with higher ADG (Coulmin, Franck, & Martin, 1982). However, no genotype-by-environment (housing) interaction is expected at the commercial level, that is, no re-ranking of the animals due to collective housing. Selection in individual cages to measure feed intake is thus a valid option to select for feed efficiency in commercial conditions. Nonetheless, these results could be different when feed is restricted, as usually in commercial farms, because of possible interactions between genotype and feeding regimens, as demonstrated by Piles et al. (2017).

4 | CONCLUSION

Our study demonstrates that selection on residual feed intake was successful to deliver a more desirable feed efficiency. Indeed, the G10 animals expressed a better feed efficiency than their G0 counterparts, but at the expense of being lighter and having a lower ADG. These results were irrespective of the type of housing of the animal, individual or collective pen, suggesting no interaction between genetic improvement for feed efficiency and housing so that selection in individual cages allows a genetic gain for rabbits raised in collective cages, commonly used in commercial farms. However, maternal effects on feed efficiency in the selected line were less favourable than in the control line, suggesting a relationship to be further examined. In practice, the impact would be very limited, as selection for feed efficiency is essentially in paternal lines, which are not used to produce maternal does at the commercial level.

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