

## MILK INTAKE IN KITS: NOT ONLY THE TOTAL AMOUNT MATTERS

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**Abstract:** The aim of this work was to identify milk intake variation patterns in kits throughout lactation, to evaluate their permanent maternal component and their relationships with the performance of kits before and after weaning. To achieve this goal, we used 73 rabbit does, controlled between the 1<sup>st</sup> and the 4<sup>th</sup> lactation, which kindled 229 litters with a total of 2225 kits. The daily milk intake records per young rabbit were analysed using a principal component analysis (PCA). We found that 72.3% of the variability was explained by the first 3 principal components (PCs). PC1 explained 46.4% of the total variability, was associated with the total amount of milk intake during lactation and presented a repeatability of 0.27 ( $P < 0.05$ ) for litters from the same female. High values of PC1 were related to higher weight of kits until slaughter age and higher feed intake during lactation and growing period. Consequently, they were related to a higher average daily gain, but a worse feed conversion ratio. PC2 explained 17.8%, was associated with the asymmetry of the milk intake (early vs. late) and presented a repeatability of 0.26 ( $P < 0.05$ ). For a given total milk intake during lactation, those with a higher milk intake in early lactation and lower during late lactation (low values of PC2) presented lower risk of death and higher feed intake during lactation. PC3 explained 8.1% of the variability, was associated with flattening of the milk intake curve and presented a repeatability of 0.05 ( $P > 0.05$ ). This component was little related to performance traits. Therefore, it seems that milk plays 2 different roles at the beginning of feed intake; the most important would affect development of the kits and thus is related with high intake. The second one, for a given total amount of milk intake during lactation, would create a kind of competition between milk and feed intake at the end of lactation. The effects of both components still persist during the growing period and seem to be moderately affected by the mother.

**Key Words:** pattern, principal component, lactation, rabbit, milk.

## INTRODUCTION

Milk intake plays an important role in the survival (Casado *et al.*, 2006) and development, not only of suckling rabbits, but also of weaned rabbits during the growing period (Szendrő *et al.*, 2002). It depends on environmental factors and also on factors related to the mother (i.e. rearing: Nizza *et al.*, 1997; genetics: El Nagar *et al.*, 2014), but seems to be little influenced by the intake capacity of the kits (Szendrő *et al.*, 2002). Although the total amount of milk ingested by the kits directly affects their weight at weaning (Lebas, 1969), the role it plays depends on their age. For example, at the onset of lactation, milk intake is more related to survival, as kits are strictly dependent on milk. At the end of lactation, it is more related to the amount of solid feed intake (Fortun-Lamothe and Gidenne, 2000; Nizza *et al.*, 2002). In this sense, high milk intake at the end of lactation would reduce feed intake before weaning and could increase the risk of digestive disorders associated with a more sudden weaning (Quevedo *et al.*, 2006). Therefore, the total amount and the evolution throughout lactation of milk intake may have an important impact on the performance of kits before and after weaning. Moreover, if there is a permanent maternal effect affecting them, the role of the mother and the strategies addressed to influence it may be relevant.

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However, information concerning the variation of milk intake curves and how this variation is related to performance traits of kits is scarce (Lebas, 1976; Casado *et al.*, 2006). Besides, no information concerning the role of the mother is available. Hence, the aim of this work was to identify variation patterns of milk intake in the kits during the whole lactation, to evaluate their permanent maternal component and their relation with the performance of kits before and after weaning.

## MATERIALS AND METHODS

The experimental procedure was approved by the Animal Welfare Ethics Committee of the Universitat Politècnica de València (UPV) and carried out following the Spanish Royal Decree 53/2013 on protection of animals used for scientific purposes, as well as the European Group on Rabbit Nutrition (Fernández-Carmona *et al.*, 2005).

The study involved 73 rabbit does, controlled between the 1<sup>st</sup> and 4<sup>th</sup> lactation, which gave birth to 229 litters with a total of 2225 kits after standardisation. Rabbit does were inseminated at 19 wk of age for the first time, and thereafter 11 d after each parturition. When they did not get pregnant they were re-inseminated again 21 d later until a maximum of three consecutive attempts. Litters were standardised at birth to 8-9 kits in the first lactation and 9-11 in the subsequent lactations. At day 17 of lactation, before kits start feed intake, they were separated from their mothers and housed in a different cage in order to control their feed and milk intake until weaning (day 28 of lactation). Diets were offered *ad libitum* for reproductive rabbit does (173 g crude protein and 185 g of acid detergent fibre per kg of dry matter) and for the growing rabbits between 17 and 56 d of age (161 g crude protein and 231 g acid detergent fibre per kg dry matter). Milk yield of rabbit does was measured 5 d a week (from day 1 to day 28 of lactation) by weighing the female before and after suckling. Litter size and litter weight were controlled at standardisation and at days 17, 28 and 56 of age. Mortality of kits was recorded daily and average individual feed intake of kits was recorded in late lactation (from day 17 to day 28) and during the growing period (from day 28 to day 56).

Although recorded by litter, all the controlled variables were expressed individually per kit taking into account the litter size at the corresponding day. Therefore, some transformations were applied to the original records. To find out the milk intake variation patterns of the kits, a principal component analysis (PCA) was applied (Lebas, 1976) using the 'PRINCOMP' procedure from SAS (2009). To evaluate the effect of milk intake on performance traits (live weight, feed intake, average daily gain and feed conversion ratio) a mixed model was used (SAS, 2009) including the number of lactation as fixed effect, the average weight of the young rabbit at standardisation and the standardised scores of the principal components (PCs) as covariates, as well as the permanent effect of the mother and the residual error as random effects. To evaluate the effect of milk intake on the survival of the kits during the different periods of their life, the 'GENMOD' procedure from SAS (2009) was used, with a binomial probability distribution and the logit transformation [ $\ln(\mu / (1-\mu))$ ] as a link function. The model included the number of lactation as fixed effect, as well as the average weight of the young rabbit at standardisation and the standardised scores of the PCs as covariates.

To find out the role of mother in the milk intake of the kits, the repeatability of PCs at different lactations was estimated. To reach this goal, the standardised scores of PCs were analysed using a mixed model (SAS, 2009) including the number of lactation as fixed effect, as well as the permanent effect of the mother [ $m$ ;  $\sim N(0, \sigma_m^2)$ ] and the residual error [ $e$ ;  $\sim N(0, \sigma_e^2)$ ] as random effects. Repeatability was evaluated as  $\sigma_m^2 / (\sigma_m^2 + \sigma_e^2)$ .

## RESULTS AND DISCUSSION

Only 2 studies have directly addressed the effect of variation in milk yield curves on performance traits of the kits by using different methodologies. Casado *et al.* (2006) modelled the lactation curves of the rabbit does and thereafter used the estimates of the parameters of the selected curve to assess their influence on litter performance. This methodology is really interesting, but it presents some problems for the purpose of the present work. Firstly, it is necessary to search for curves that could be fitted, which is reasonable for milk yield of the rabbit doe, but not so clear for milk intake of kits (e.g. survival rate of the litter could affect the amount of milk one kit could suckle from its mother, modifying the shape of the milk intake curves). Secondly, it presents some statistical problems, as we would use the estimates of the curve parameters to evaluate their impact on the performance of the young rabbit. Finally, and most important, as the parameters are not necessarily independent, a change in one parameter could imply a

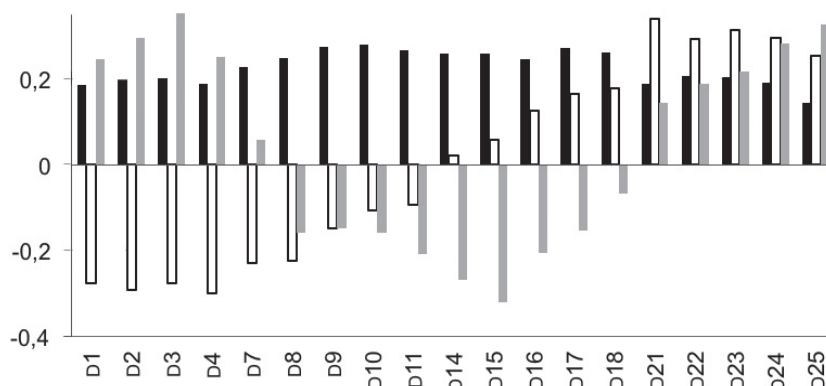
change of the moment of intake but also in the total intake, so we would be unable to distinguish clearly between the whole amount of milk intake and the effect of the distribution throughout lactation.

On the other hand, Lebas (1976) used a PCA to address the issue, but only studied the litter weight at weaning. PCA allows us to synthesise the information coming from a numerous set of correlated variables into a smaller set of new independent variables (PCs) ordered according to the variability they explain. Thus, with a small subset of them it is possible to explain a very large amount of variability of the original variables. Furthermore, many times these PCs can be biologically interpreted, as they are calculated as linear combinations of the original variables searching for specific goals.

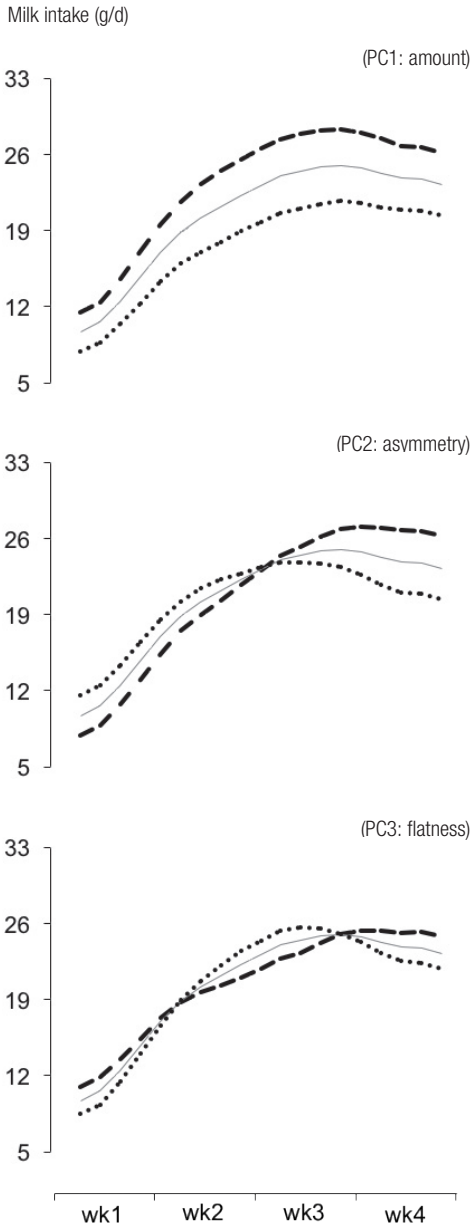
### Identification and interpretation of patterns of variation

In our dataset, 72.3% of the variation of milk intake was explained by the first three PCs. Figure 1 represents the relation among milk intake at a particular day and the scores of the first three PCs (the bigger the bar, the stronger the relation; if the value is higher than zero the relation is positive, and if the value is lower than zero the relation is negative). PC1 explained 46.4% of total variability. The fact that all the bars are positive indicates that PC1 could be interpreted as a measure of the total milk intake during lactation. In fact, the estimated correlation between PC1 and the total milk intake during lactation was +0.99. PC2 explained 17.8% of the total variability and could be interpreted as the contrast between the early and the late intake (or the asymmetry with respect to the mean curve). Thus, for a similar amount of total milk intake, high scores of PC2 indicate lower milk intake at the beginning and higher at the end of lactation in comparison with the mean curve. PC3 explained 8.1% of the total variability and could be interpreted as the flattening with respect to the mean curve: higher PC3 scores indicate flatter curves of milk intake. Lebas (1976) found, for the milk intake of kits, an analogous interpretation of the PCs with a similar proportion of explained variance (PC1 explained 45.2%, PC2 15.1% and PC3 6.7% of the total variability). Thus, it could be concluded that the sources of variation in milk intake were kept constant independently of genetics, place or time.

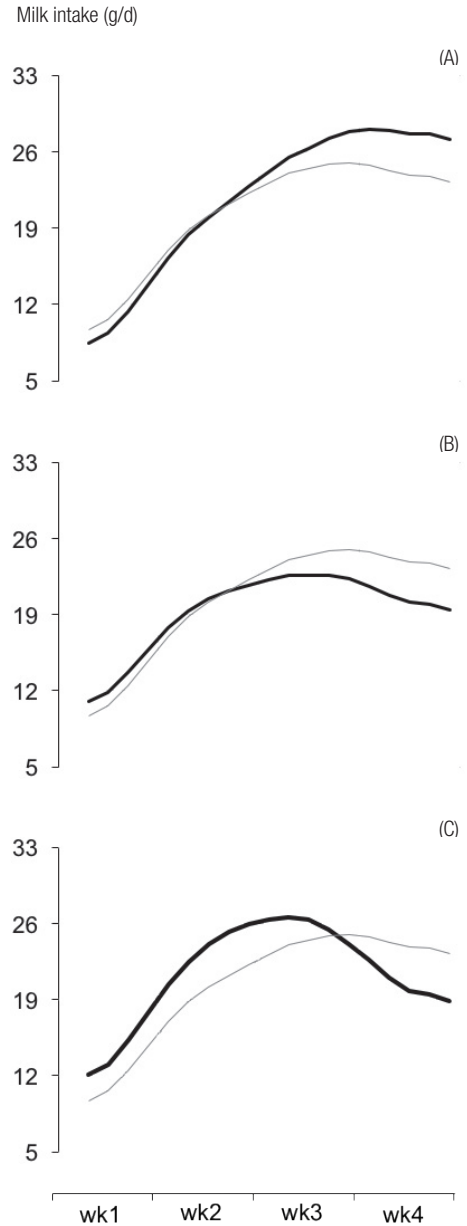
However, based on the previous description it is not easy to figure out what the change in a milk intake curve would be as a result of a change in the score in one PC. Figure 2 represents the milk intake curves associated with a change by  $\pm 1\sigma$  in the scores of the first three PCs. It is interesting to point out the consequences of the variability that each PC explains on the associated curves. For the same dimensionless change ( $\pm 1\sigma$ ), the higher the value of the PC, the closer the associated curves are to the mean curve. On the other hand, Figure 2 is just a representation of the way the curves change according to the patterns of variation; nevertheless, 'real' curves would be defined by the scores of three PCs. Figure 3 shows some milk intake curves associated with different scores of PCs. It can be seen that it is possible to represent a large amount of milk intake curves by using the scores of the three PCs. For example,



**Figure 1:** Eigenvectors of the first 3 principal components (PCs). Relationship between individual daily milk intake and the PCs score. ■, PC1 (Total milk intake during lactation); □, PC2 (asymmetry of the milk intake curve); ▒, PC3 (Flatness of the milk intake curve).



**Figure 2:** Milk intake curves associated to variability in the scores of the principal components (PCs). —: Mean curve. ---: curve associated to a change compared to the mean of  $+1\sigma$  in the corresponding PC. ....: curve associated to a change compared to the mean of  $-1\sigma$  in the corresponding PC. PC1: Total milk intake during lactation, PC2: asymmetry of the milk intake curve, PC3: Flatness of the milk intake curve.



**Figure 3:** Milk intake curves associated with different scores of the first three principal components (PCs). —: is the mean curve. —: is the curve associated to scores compared to the mean of:  
 A)  $+1/3\sigma_{PC1}$  in PC1 and  $+1\sigma_{PC2}$  in PC2  
 B)  $-1/3\sigma_{PC1}$  in PC1 and  $-1\sigma_{PC2}$  in PC2  
 C)  $+0.5\sigma_{PC1}$  in PC1 and  $-1.5\sigma_{PC2}$  in PC2 and  $-1\sigma_{PC3}$  in PC3

Figure 3.B represents the milk intake curve of a kit with an intake slightly lower than the mean ( $-1/3\sigma$ ), but not equally distributed throughout time ( $-1\sigma$ =higher than the mean at the beginning and lower at the end of lactation).

### Relation between patterns of variation and performance traits

Many times when we assess the way a large set of correlated variables (i.e. time dependent series such as milk yield, feed intake, etc.), influence another variable, we have to cope with problems related to 'the Curse of Dimensionality' (sparsity of samples, multicollinearity among variables, exploding number of models and the effect of noise; Clarke *et al.*, 2009). In general, we tend to simplify the problem by summing or averaging variables into larger periods. Although this is reasonable, there is a waste of information because we are studying only one source of variation (the sum or the average). For example, in the present work, if we wanted to evaluate the effect of milk intake on the performance of the kits and intended to study it by measuring the total amount of milk intake, we would have simplified the study by explaining 46.4% of the variability, but the effects of 53.6% of the variability would have remained unexplored. On the contrary, using the PCA it was possible to split the information into three sources of variation, allowing us to explore the effects of 25.9% more of the variability. The relations among each of the PCs and the performance traits of growing rabbits is presented in Table 1.

To make interpretation easier, we can imagine that the values presented in the table are the estimated differences between animals with a milk intake curve like the dashed curves (Mean curve+ $1\sigma_{PC1}$ ) and animals with a milk intake curve like the grey continuous curves (Mean curve) in Figure 2. For example, the estimated weight at day 17 of lactation of animals with a milk intake like the dashed curve in PC1 of Figure 2 was  $30.4\pm 0.95$  g higher than the mean. In agreement with the results reported by Lebas (1976) and Szendrő *et al.* (2002), the total amount of milk intake (PC1) had an important effect on the rabbit live weights at the three controlled ages. Nevertheless, this effect decreased with age; at day 17, 28 and 56 an increase of  $\sigma_{PC1}$  had an effect of +12.3, +11.8 and +6% on live weight, respectively. On the other hand, the rabbit weights were little influenced by asymmetry (PC2) or flattening (PC3). This latter result is not in agreement with Lebas (1976), who showed that curves with a fast increasing and decreasing (high PC3) improved litter weight at weaning.

Regarding feed intake before weaning, the higher the total amount of milk intake (PC1), the higher was the solid feed intake. This positive effect on feed intake could be associated with the higher weight and maturity of kits (Szendrő *et al.*, 2002). On the other hand, the asymmetry (PC2) also had an important influence on the starting of feed intake. For a similar total amount of milk intake, the higher the milk intake was at the end of lactation (asymmetry  $>0$ ), the lower was feed intake (hypothetically also with a lower development of the intestinal tract). This result is in agreement with those reported by Fortun-Lamothe and Gidenne (2000), Nizza *et al.* (2002) and Di Meo *et al.* (2003), who showed that for rabbits with a similar weight at the beginning of feed intake, high milk intake during late lactation is related to low feed intake. Reciprocally, we observed that, for a similar total amount of milk intake, the higher the milk intake during early lactation (asymmetry  $<0$ ), the higher the feed intake will be. Therefore, milk plays two different roles in the beginning of feed intake. The most important consists of promoting the development of the kits and consequently

**Table 1:** Mean and response per unit of standard deviation in the score of the first three principal components on performance traits. Mean or regression coefficients plus standard error in brackets.

	Live weight (g)			Feed intake (g DM/d)		ADG (g/d)	FCR (kg/kg)
	17 d	28 d	56 d	17-28 d	28-56 d	28-56 d	28-56 d
Mean	248(1.7)*	439(5.1)*	1655(11)*	3.9(0.22)*	79(1.1)*	43.4(0.29)*	1.84(0.026)*
Amount <sup>1</sup>	30.4(0.95)*	52(2.9)*	100(7.1)*	0.7(0.13)*	4.8(0.73)*	1.7(0.21)*	0.04(0.014)*
Asymmetry <sup>2</sup>	-2.8(0.95)*	5(2.9)	20(7.0)*	-0.5(0.12)*	-0.3(0.72)	0.5(0.21)*	-0.03(0.014)*
Flatness <sup>3</sup>	-4.8(0.88)*	1(2.7)	-7(6.7)	-0.1(0.12)	-0.8(0.70)	-0.3(0.20)	0.00(0.013)

ADG: average daily gain; FCR: feed conversion ratio; DM: dry matter.

<sup>1</sup>Interpretation of PC1: total amount milk intake during lactation.

<sup>2</sup>Interpretation of PC2: asymmetry of the curve, for a similar total amount of milk intake, the higher is the value, the later is the milk intake.

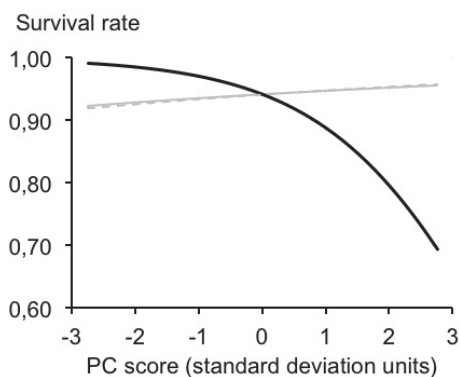
<sup>3</sup>Interpretation of PC3: flatness of the curve, for a similar total amount of milk intake, the higher is the value, the flatter is the curve.

\*Values differ significantly from zero ( $P<0.05$ ).

feed intake. The second, for a given total amount of milk intake during lactation, is determining a competition between milk and feed intake at the end of lactation.

Many of the effects of milk intake during lactation still persisted during the growing period. Total amount of milk intake (PC1) was relevantly related with higher feed intake during the growing period and consequently with a higher average daily gain. However, although the effect was not very important, feed conversion ratio (FCR) was higher. These results are in agreement with Szendrő *et al.* (2002), who suggested that the higher the milk intake, the higher the development of the digestive tract at weaning and consequently the higher the feed intake and growth during the growing period. However, when comparing at the same age, they found a much higher feed intake in animals with high milk intake (higher FCR). On the other hand, when comparing at the same slaughter weight, they showed that FCR was lower, as these animals reached the slaughter weight 9 d before. Thus, the higher FCR at the same age of animals with high milk intake could be associated with their higher weight during the growing period and, consequently, higher nutrient expenses for maintenance. Regarding to the asymmetry (PC2), no significant effect on feed intake during the growing period was observed. Although small, significant and non-negligible effects of PC2 on average daily gain and FCR were observed. If we considered that the mortality rate of kits during lactation was associated with asymmetry (see below), the relation between asymmetry and performance traits during the growing period could be associated with mortality during lactation; for example, if animals with a higher average daily gain and lower feed efficiency survived more easily during lactation.

Milk intake only had an effect on survival rate during the early lactation (0-17 d). Figure 4 represents the estimated survival rate during this period depending on the scores of the PCs. It can be seen clearly that asymmetry of milk intake was highly related with survival rate during early lactation. For a similar total milk intake, the lower the early milk intake, the higher the risk of death. Surprisingly, no significant effect of total amount of milk intake (PC1) was observed. However, it is necessary to point out that survival rate can change total milk intake cancelling its effect, due to the fact that animals surviving low early milk intake had more milk available which would have allowed them to have a high total milk intake (high PC1). Thus, for similar values of PC1 higher than zero, it is possible to find litters with low mortality because their mothers yield more milk and litters with high mortality that ingested more milk because their litter mates did not survive. Therefore, it seems that mortality changes the asymmetry of the intake, instead of the opposite. Anyhow, it seems clear that survival rate is defined by the amount of milk at the beginning of lactation (Casado *et al.*, 2006). Finally, the milk intake curve of one litter would be the consequence of their survival rate and



**Figure 4:** Estimated survival rate of the kits during early lactation (0-17 d) as a function of the score of the principal components (PCs) obtained for individual daily milk intake. —: PC1 (Total milk intake during lactation), —: PC2 (asymmetry of the milk intake curve). - - -: PC3 (Flatness of the milk intake curve).

the milk yield curve of the mother. On the other hand, no significant effects of milk intake on survival rate during the growing period were observed, probably because overall mortality was low (8%), as well as the fact that kits with high PC2 (having low early milk intake) that were able to survive were probably stronger than others with a low PC2. Therefore, the results of the present work did not allow us to elucidate or refute any hypothesis regarding the effects of milk intake on the risk of death during the growing period.

### ***The role of the mother and strategies affecting it***

Milk yield of the mother and consequently milk intake of the kits depend on factors related to the mother and environmental temporary factors. Repeatability of PCs (ranging from 0 to 1) is a way to study the role of the mother, as it is the proportion of the permanent maternal effect variance with respect to the total variance of the PC. In a given environment, the higher the repeatability, the higher the difference between females and consequently, the higher is the role of the mother. The lower the repeatability, the higher the influence of

temporary environment. For litters from the same mother, repeatability of PCs was 0.27 ( $P < 0.05$ ), 0.26 ( $P < 0.05$ ) and 0.05 ( $P > 0.05$ ) for PC1, PC2 and PC3, respectively. This result indicates that the PC1 and PC2 scores of litters from the same mother are correlated among them. Moreover, it suggests that, for total amount and asymmetry of milk intake, the role of the mother is moderated (repeatability  $< 0.30$ ) and the temporary environment is important. On the contrary, no evidence for repeatability higher than zero was found for flattening, suggesting that this source of variation in the milk intake is mainly environmentally driven.

The moderate role of the mother for total amount and asymmetry of milk intake suggests that strategies shifting the permanent maternal effect could have a relevant impact on total amount and asymmetry of milk intake and consequently on growth and development of the kits. The permanent maternal effect is comprised of permanent environment and genetics of the mother (in fact, repeatability is the theoretical maximum value for heritability before its estimation). A possible strategy to affect the permanent environment in a controlled way could be through the reproductive rhythm or through nutrition (the diet offered during rearing or the reproductive life of rabbit females). On the other hand, the fact that total amount (PC1) and asymmetry (PC2) of milk intake could have a genetic background does not necessarily mean that we have to select for these traits, as it would be extremely expensive compared to the economical weight they might have, but selection could affect them. Selection for a specific trait, in the long term, could shape the lactation curve of females and consequently the milk intake curve of their kits depending on the criteria animals have been selected for (Saviotto *et al.*, 2014).

## CONCLUSIONS

Regarding the three sources of variation found for milk intake, the two most important (total amount of milk intake and asymmetry of the milk intake curve) presented a moderated role of the mother, which means that strategies such as the feeding programme or genetic selection could affect them. The total amount of milk intake seems to be the main factor affecting the performance of kits. However, asymmetry was mainly related to survival during early lactation and could be associated with different patterns of development before weaning, which could influence the performance during the growing period. On the other hand, milk seems to play two different roles at the onset of feed intake; the most important would affect the development of the kits and thus would promote solid intake. The second one, for a given total amount of milk intake during lactation, would create a kind of competition between milk and feed intake at the end of lactation.

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