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GENETIC SELECTION AND NUTRITIVE RESOURCES ALLOCATION IN REPRODUCTIVE RABBIT DOES

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ABSTRACT

In the present work is analysed how frequent feeding and selection programmes could be affecting resources allocation in reproductive rabbit does, and the possible consequences resulted from these changes, as well as the central role of body condition for a suitable female performance considering genetic level, health and welfare. Resources allocation between functions, and consequently body condition, must be genetically driven. Traditional view of body reserves mobilisation in reproductive rabbit does as a response of feed intake must be moved to an animal view, where feed intake must be considered more as an “output” consequence of the resources allocation in the female to ensure current and future litter viability. To a great extent, future reproductive potential of reproductive rabbit females is decided before first partum. There seems to be enough evidence of a possible threshold for the rabbit female birth weight to reach the beginning of reproductive life in a suitable body condition to maximise their future reproductive potential. The moment of first mating could be identified the last ‘pure’ data of the animal, sign of the animal soma and probably related to their productive potential. The choice of an adequate feeding system during rearing and first pregnancy also seems to be relevant in the reproductive performance of rabbit females in the short and long term. This should allow young females to reach first mating and late pregnancy with a good maturity level, but over-fattening must be avoided to reduce the risk of pregnancy toxaemia and reduced reproduction. The body condition of the females changes during the reproductive cycle and throughout their reproductive life according to their genetically determined level. The problems appear when the animals are forced to differ from this adequate level, increasing susceptibility to disease, other stress factors and eventual failure. The body condition of young rabbit females reaches the peak 10 days before kindling. From this moment to kindling, reproductive rabbit does seem to suffer the highest mobilisation of body reserves, with the body condition showing the lowest level at partum. Negative energy balances detected during lactation do not seem to have the strength of those observed in late pregnancy. Genetic selection in rabbit by litter size at weaning has increased prolificacy but also the ability to obtain resources (more feed intake at the onset of lactation, better energy utilisation during pregnancy), without compromising the survival of rabbit females. However, it could also have increased the sensibility of animals to the environment, addressing more the maternal investment to the future litter respect to the actual under restricted conditions to maximize their selection success “the number”. Rabbit does selected for reproductive longevity have a greater soma (body weight and body condition), which enables them to better cope with the possible productive challenges that they may meet in the course of their productive life. There is also evidence that they have greater plasticity in using their soma, making them more robust to overcome demanding situations. In fact, the response to environment restriction of females coming from a line founded for reproductive longevity criteria was flatter than those obtained for females selected for litter size at weaning in all the traits controlled, highlighting their differences on robustness. In addition, it seems to be evidence of a possible improvement of the immune system modulation in robust animals (lower sensitivity to immunological challenges), although further research effort must be done in the future to confirm this matter.

Keywords: Rabbit female, rearing management, genetic selection, nutrient partitioning, body condition.

INTRODUCTION

Rabbit health may be considered one of the main handicaps to current rabbit production under commercial conditions. Rabbit susceptibility to diseases is similar to other intensively farmed animals such as pigs, with similar on-farm mortality risk (Lebas, 2000; Rosell and de la Fuente, 2009). However, the appearance of a new challenge in minor species, such as epizootic rabbit enteropathy (ERE), usually requires devoting a greater part of the scientific effort to reduce their economical impact. For example, many works have focused on increasing the knowledge of the influence of nutrition on intestinal health of growing rabbits in recent years, with the main results recently being included in acknowledged revisions (Gidenne and Garcia, 2006; Carabaño *et al.*, 2008, 2009).

In any case, this effort should not lead us away from the study of the current breeding systems for reproductive rabbit does could be unbalancing nutrient partitioning, impacting on the global health and welfare of the farm, and their possible implication in the incidence of specific illnesses. In the last two decades, we have moved on from more or less traditional production systems to other, more intensive ones using modern prolific lines, which have made the adjustment of the nutritional requirements of the animals necessary in line with the new demands (Maertens, 1992). It is true that the nutritional requirements of weaned rabbit have changed as a result of selection by growth rate - between +0.45 and 1.23 g/day per generation of selection - although it is the reproductive does that have suffered the effects of these improvements achieved and the new production systems to a greater extent.

Genetic selection programmes in reproductive rabbit does have mainly focused on improving litter size, either at partum or weaning. These programmes bring about an effective increase of between 0.05 and 0.13 live-born kits per generation of selection (Rochambeau *et al.*, 1994; Gómez *et al.*, 1996). This selection criterion, along with artificial insemination (AI) of the does with semen from males selected for growth rate, has clearly increased the litter's demand for milk. On the other hand, the frequent intensification of the reproductive rhythms gives rise to competition between the mammary glands and foetuses, which is usually detrimental to foetal growth if the needs are not well covered (Fortun and Lebas, 1994). The requirements of reproductive rabbit does may therefore have increased considerably in recent years, affecting nutrient partitioning and perhaps compromising body condition, lifespan and general health of the farm.

In this sense, some recent works have even suggested a possible effect of doe health status on the potential risk of their kits suffering digestive troubles during the growing period. Quevedo *et al.* (2003), in a trial with five thousand kits from five reproductive cycles, described an increase in mortality during the growing period with the mother's age (from 5 to 29%), with 22% of females being responsible for 50% of the mortality observed. In fact, Garcia *et al.* (2005) observed a significant effect of the litter on the microbiotic profile of young rabbits, with siblings showing a high similarity rate.

For this reason and in the current productive context, new breeding systems must be defined with more emphasis on the welfare of the animals and the general health status of the farm. The search for long-term and globalised strategies to uphold these criteria would take into account the possible collateral effects resulting from isolated strategies (Pascual, 2004). A suitable strategy for the feeding and genetic selection of reproductive does would therefore have to consider short-term productive criteria - such as litter size, milk production or the interval between parturitions - as well as long-term - for example body condition, life expectancy and health status of the doe - while evaluating the possible effect on subsequent litter development (transition at weaning, gastrointestinal health...).

Both reproduction (litter size, milk yield, fertility…) and survival (health, welfare, lifespan…) are energetically expensive. Especially in mammals, body reserves are involved both in successful reproduction and in maintaining the soma and thereby survival (Theilgaard, 2006). Thus, the body condition of the rabbit females might be an important factor when addressing the association between reproduction and survival, and consequently may play a central role in the definition of their adequate genetic selection programmes. In the present work is analysed how frequent feeding and selection programmes could be affecting resources allocation in reproductive rabbit does, and the possible consequences resulted from these changes, as well as the central role of body condition for a suitable female performance considering genetic level, health and welfare.

NUTRIENT PARTITIONING

The different metabolic functions of a rabbit female (growth, gestation, milking, health…) must be covered from the available resources (food or body reserves), and the processes by which available nutrients are channelled, in varying proportions, to these functions is known as nutrient partitioning (Friggens and Newbold, 2007). Nutrient partitioning changes in function of the physiological stage, with linked changes in the endocrine profile (Bauman, 2000) which also controls body fatness throughout the reproductive cycle (Vernon *et al.*, 2001), and with the age of the animal, as relative priorities of the females for the different life functions changes through animal's life (Martin and Sauvant, 2010). Thus, it is well-accepted that resources allocation between functions, and consequently body condition, must be genetically driven.

Although mobilisation could be environmentally driven (*e.g.* when voluntary feed intake is limited under heat stress conditions), there exists a lot of evidence of the independence between nutrient availability and mobilisation. In fact, there are numerous studies where additional energy supply by dietary energy enrichment has not yielded appreciable results to avoid reserves mobilisation in cows (Gagliostro and Chilliard, 1991; Andersen *et al.*, 2003), but also in rabbits (Fortun-Lamothe, 1997; Xiccato *et al.*, 1999; Pascual *et al.*, 2000, 2003). Instead, when the feed intake was successfully increased, this extra energy boost is frequently addressed to milk production (Xiccato *et al.*, 1995; Parigi-Bini *et al.*, 1996). For example, the traditional view is that primiparous rabbit does have limited there voluntary feed intake, as their growth is not completed, that could lead to body reserves mobilisation during lactation (Xiccato, 1996; Pascual *et al.*, 2003; Fortun-Lamothe, 2006). However, there does not seem to be a relevant relationship between body weight (BW) and daily feed intake during the first lactation (Figure 1), showing primiparous does differing 1 kg BW a similar feed intake.

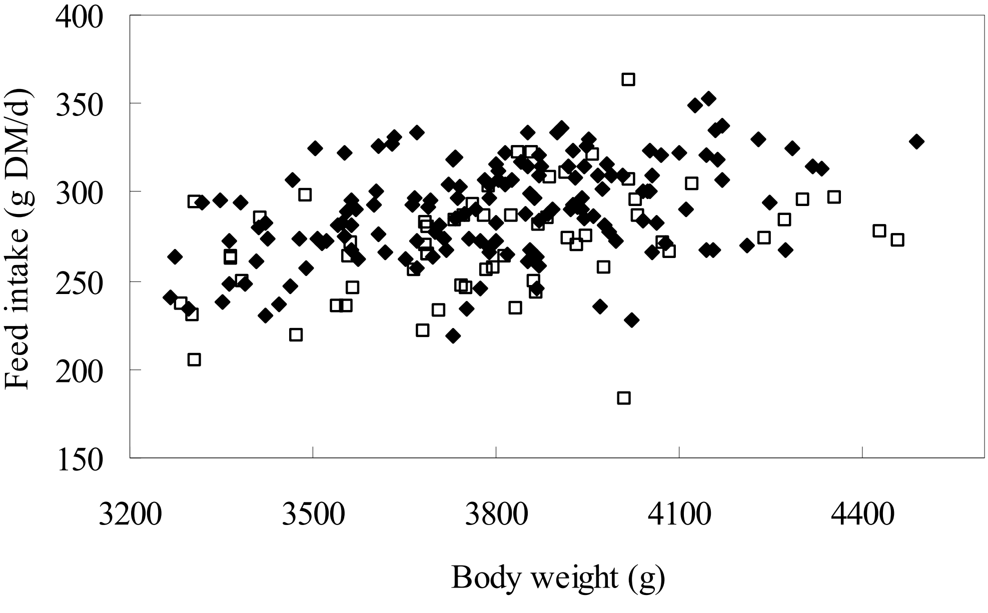


Figure1: Relationship between dry matter intake (g DM/d) and body weight (g) of primiparous rabbit does (data from ☐ Pascual *et al.*, 2002b and ◆ Quevedo *et al.*, 2006b).

If we accept that there is a genetic component driving temporal changing of body reserves, evaluation of punctual negative energy balances in rabbit females must not be only done as a malfunctioning of the animal, but as a possible natural adaptation done to maximize her chances of evolutionary success (Friggens and Newbold, 2007). From an evolutionary point of view, rabbit selection has been addressed to maximise the number of viable litters produced in a lifetime. To achieve this goal, it must be defined the optimal trade-off between number of pregnancies and postnatal investment in litter viability (Friggens, 2003), i.e. the optimal trade-off between the maternal investment addressed to the current and the future litter.

Rabbit female usually have a great decision making ability to be or no to be pregnant in function of the resources availability, which could also assisted by hormonal and biostimulation methods (Theau-Clément, 2007). However, female doesn't know the future available resources when the reproduction effort will be increased (end of pregnancy and beginning of lactation). Thus, pregnant doe store reserves for the forthcoming litter (similar to other mammals; Oftedal, 2000) as resources available for foetal growth and early suckling will affect clearly litter chances of survival. Body reserves mobilisation observed around parturition is mainly addressed to this task (Savietto, 2012), and it seems to be independent of the resources available at this moment, as additional fatness was performed to be transfer to the litter and maintaining a heavier soma is energetically costly, reduce mobility and increase the risk of predated (McNamara and Houston, 1990). On the other hand, yielding more milk of that required at the end of lactation will not improve the litter's chances of survival. Therefore, milk yield is decreased as the priority to restore reserves for the future litter start to increase.

Given these considerations, under no-limiting resources conditions, traditional view of body reserves mobilisation in reproductive rabbit does as a response of feed intake must be moved to an animal view, where feed intake must be considered more as an "output" consequence of the resources allocation in the female to ensure current and future litter viability. This new view has been used in the present work to evaluate how rearing, feeding and genetic selection programmes could be affecting both body conditioning and nutrient partitioning, and their possible effect on reproduction and lifespan.

YOUNG RABBIT FEMALES

As was expected, many works on nutrition have addressed the adequate nutrition of rabbit does during their reproductive period (from first parturition to the moment of culling or death), and have frequently been reviewed (Xiccato, 1996; Pascual *et* al., 2003). However, to a great extent the future reproductive potential of these females could be decided before first parturition (during their own gestation, lactation, growth and rearing). Reaching certain crucial points in the reproductive life of the females with adequate BW, body conditioning, health status, well-being and soma will be essential in the definition of their future reproductive performance, health and lifespan. Among these crucial milestones may be highlight the birth weight, the maturity of the female at first mating day and the rearing feeding programme used.

Birth weight

There is sufficient evidence of the negative consequences of a deficient foetal nutrition on adult reproductive performance (McEvoy and Robinson, 2003). In sheep, Gunn *et al.* (1995) observed that either foetal or early life undernutrition reduced adult reproductive performance, inferring from their data that impaired reproductive performance was mediated through reduced embryo survival. In addition, Yakovleva *et al.* (1997) described that not only ovarian but also adrenal function was compromised in prepubertal and adult female progeny of water voles (*Arvicola terrestris*) that suffered food deprivation in early pregnancy.

In multiparous species such as rabbits, the risk of an early undernutrition rises as a result of the greater competition for nutrients both during pregnancy (ovulation rate, situation in the abdominal cavity, placenta irrigation…) and lactation (litter size, number of teats, milk yield…), which could affect the adequate development of the young female. In fact, some recent trials (Biró-Németh and Szendrõ, 1990; Poigner *et al.*, 2000; Szendrõ *et al.*, 2006; Savietto *et al.,* 2010; Martínez-Paredes *et al.*, 2009) have observed a worsening of reproductive performance traits of rabbit females and males when an early undernutrition was foreseeable. This worsening seems to be more related to the birth weight than to the size of the litter in which the animal was reared (Poigner *et al.*, 2000; Savietto *et al.*, 2009; Martínez-Paredes *et al.*, 2009), although both the amount milk and feed received during their rearing significantly affects their performance at the age of the first mating (Rommers *et al.*, 2001; Szendrõ *et al.*, 2006). Recently, Savietto *et al.* (2010) proposed a possible threshold for the female birth weight that allows them to reach the beginning of their reproductive life in an adequate body condition, which could maximise their future reproductive potential (Figure 2).

In this same way, Poigner *et al.* (2000) observed that the higher the birth weight of the females, the larger the litter size of their offspring (+12.4%) was during 6 consecutive reproductive cycles. In a line of bucks selected for growth rate (Martínez-Paredes *et al.*, 2009), when comparing bucks with different birth weight and further growth rate it was observed that those bucks with the lowest BW at birth and the highest growth rate afterwards (perhaps an indicator of a possible foetal undernutrition) had the lowest number of ejaculates and the highest percentage of abnormalities (P<0.05).

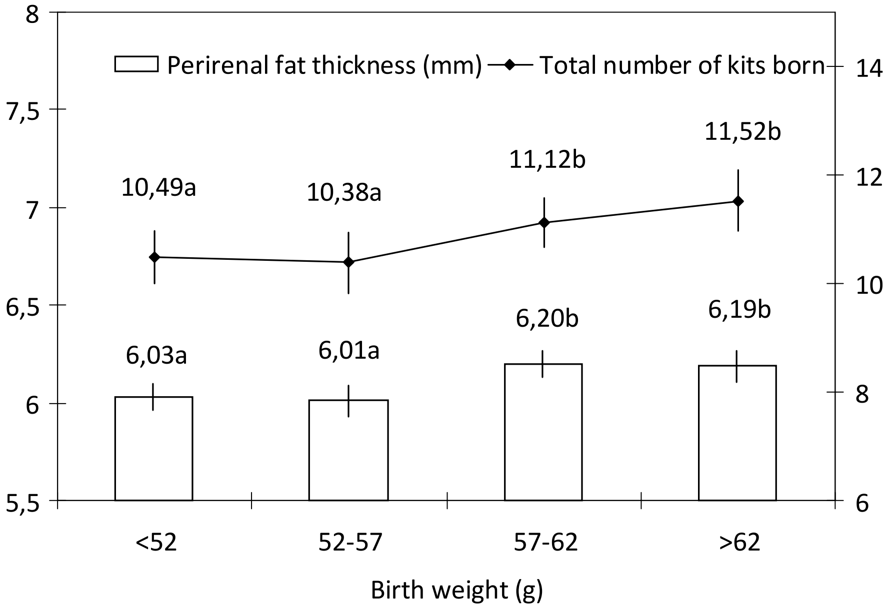


Figure 2: Effect of birth weight of females on their perirenal fat thickness at first mating and litter size at birth (total born) in their two first litters (Savietto *et al.*, 2010).

The possible disadvantage of reducing birth weight in the subsequent adult reproductive potential of the females should be considered in the new genetic selection programmes for multiparous species. Unfavourable genetic correlation seems to be observed between number of piglets born alive and within-litter birth weight variability (Damgaard *et al.*, 2003; Wolf *et al.*, 2008). Therefore, genetic selection for litter size, which although it increases litter weight at birth, reduces the individual birth weight (Moce and Santacreu, 2010), could provoke a negative effect on birth weight heterogeneity. Poigner *et al.* (2000) observed that females born with lower BW were also born in significantly larger litters (11.2 kits) than those born with higher BW (8.8 kits). In any case, Argente *et al.* (1999) did not find phenotypic correlation between litter size and the within-litter variability in birth weight.

Maturity at first mating

As can be seen in Figure 3, the total body energy of the young rabbit female increased linearly from 9 weeks of age to the end of first pregnancy, when a clear drop occurred until the first parturition (Pascual, personal communication). However, this graphic corresponds to the average of several females, with the evolution showing a great variability in terms of the animal (genetic effects), feeding programme and age at first mating.

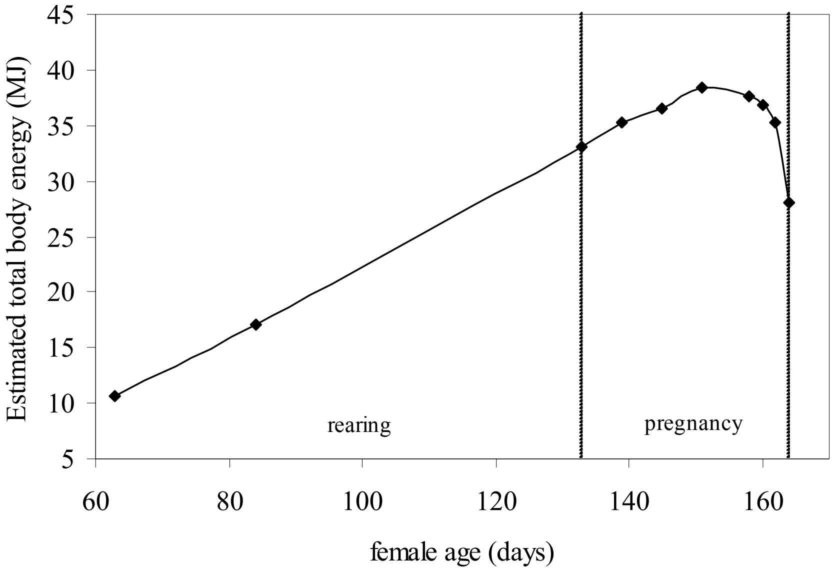


Figure 3: Evolution of the estimated total body energy of young rabbit females during the rearing period and first pregnancy (Pascual, personal communication).

The moment of first mating has been frequently identified as a crucial point in the development of the young female. This is the last ’pure’ data of the animal, sign of the animal soma and probably related to the productive potential. From this moment on, all their records will be conditioned by their reproductive history.

In gilts, although the effect of body condition before first partition on the reproductive life is still unclear, many works suggest that when the fatness of the female deviates from the ’optimum level’ at first mating there are negative consequences on reproduction. O’Downd *et al.* (1997) observed how those nutritional strategies intended to increase body fat reserves in genetically lean young breeding sows improved their fertility and lifespan. In a fat swine line, Tarrés *et al.* (2006) proposed the existence of an optimal female body condition at first farrowing to maximise longevity, recommending that backfat thickness should be more than 16 mm at the end of the rearing period and maintain this level until the first parturition without exceeding 19 mm. In fact, an excessive fatness at first mating has been also related to a reduced longevity, with moderate feeding restriction being recommended during the rearing period of gilts (Jørgensen and Sørensen, 1998). In other studies, gilt backfat obtained from field test performance before first parturition has been reported to have no effect on reproductive life (Yazdi *et al.*, 2000 a), but to have positive phenotypic (Yazdi *et al.*, 2000 b) and genetic effects (López-Serrano *et al.*, 2000).

Similar results have been found for young rabbit females. Quevedo *et al.* (2005) compared two types of crossbreed rabbit does (old and current) obtained from the cross of different generations of maternal lines (12 generations) selected for litter size at weaning (Table 1). Twelve generations of selection for prolificacy increased the perirenal fat thickness of young females at three months of age, although differences between animals disappeared as of this point. As was expected, the selection for prolificacy resulted in increased litter sizes at birth of the current generation (Quevedo *et al.*, 2005 and 2006a) compared with the old one (+1.1 total kits born in average; $P<0.05$). For these same animals, Theilgaard *et al.* (2006) described that, although no significant effect of selection for litter size at weaning on reproductive lifespan was observed, a tendency towards longer survival in the current population was indicated (Table 1).

This result is at least surprising, since resources allocation theories explain that higher reproduction has an antagonistic effect on longevity as more resources are directed to reproduction and consequently less is available to the longevity (Kirkwood and Austad, 2000; Mysterud *et al.*, 2002). The trend for higher longevity in current population with the highest reproductive potential could mean that selection for litter size has not only increased the genetic level for litter size but may also have changed the ability to acquire resources (Noordwijk and de Jong, 1986; Reznick *et al.*, 2002). The higher body condition at the onset of their reproductive life could be an indicator of this ability.

Table 1. Effect of selection for litter size at weaning on the body condition of young rabbit females and their subsequent reproductive performance and risk of culling during 5 reproductive cycles (adapted Quevedo *et al.*, 2005; 2006a; Theilgaard *et al.*, 2006).

Type of females	Old[1]	Current
Crosses done to obtain the females	Line V (15th gen.) × Line A (16th gen.)	Line V (26th gen.) × Line A (29th gen.)
Perirenal fat thickness at 3 months of age (mm)	8.06±0.14^a	8.36±0.15^b
Total nº born at 1st partum	8.86±0.52^a	10.76±0.53^b
Total nº born (average 2nd to 5th partum)	10.30±0.44^a	11.39±0.45^b
Relative risk of culling[2]	1.00	0.64

[1] Old animals were obtained from cryopreserved animals from earlier generations of the same lines that were thawed and transferred to obtain live adults contemporary to the current generation.
[2] Relative risk of being culled during 5 reproductive cycles P=0.12.
[a,b] Measures without letters in common are significantly different to P<0.05.

Other works done with young rabbit females have provided evidence of the relevant role of body fatness at the beginning of reproductive life in mediating the tradeoffs between reproduction and longevity. Rommers *et al.* (2002) observed how heavier rabbit females at 14.5 weeks of age remained so throughout the reproductive period and improved litter size only at the first parity (8.9, 7.7 and 6.4 total kits born for heavy, medium and small does, respectively). In another work, Rommers *et al.* (2004a) reported additional results about the relevance of young rabbit female maturity level when they reach the moment of first mating. The authors proposed that reproductive performance could be improved by restricted feeding during rearing and extended first insemination, allowing the female to reach this point with an adequate maturity level.

Rearing feeding programmes

Under commercial conditions, females destined to reproduction usually receive a fattening feed *ad libitum* until slaughter date, and then a restricted feed for reproductive does (approximately 140 g per day) until the first kindling, in order to avoid excessive fattening of the animal, high perinatal mortality, a possible decrease of voluntary consumption at the onset of lactation and a diminution of the lifespan of the doe (Partridge, 1986; Maertens, 1992). However, some recent works show that restriction during rearing can lead to a reduction of female maturity at the first insemination (Rommers *et al.*, 2004b). The insemination of these animals of lower BW has been related to a lower fertility (Szendro *et al.*, 2002) and smaller litter size at the first parturition (Rommers *et al.*, 2001 and 2002), with a possible reduction in the milk production of the does. However, in some cases the differences in BW and productivity seem to disappear in the successive cycles. From these data, it seems that the BW, body condition and age of young rabbit females at first mating could be very important to avoid the cited problems independently of the feeding programme used.

An alternative to restriction could be the use of fibrous feed *ad libitum* which, besides avoiding an excessive fattening of the does at first parturition, could increase the ingestion capacity of primiparous does. In fact, Lebas *et al.* (1982), García *et al.* (1995) and Fernández-Carmona *et al.* (1998) observed that younger animals fed with fibrous feeds showed a higher weight of digestive tract and contents. As may be observed in Table 2, several works have been carried out to try to stimulate the feed intake of reproductive does during the first lactations by the inclusion of fibrous feeds administered *ad libitum* in the rearing period, with different responses being observed depending on the feed used and the moment of application.

From these works, it can be deduced that the inclusion of fibrous diets in rearing would have to take place as soon as possible, and not much beyond 60-70 days of life. When fibrous diet is included later, to avoid a delay in the growth of young does, it does not seem to affect the digestive tract development in the same way and no differences are observed in the productivity of the reproductive does (Quevedo *et al.*, 2005; Verdelhan *et al.*, 2005). On the other hand, the largest increases in female intake during lactation (+ 11-18%) were observed with the rearing diets that showed an NDF content of over 40% in DM, although Pereda (2010) did not observe any change in lactating feed intake of females receiving a diet with 50.5% NDF during rearing.

Table 2. Use of fibrous feeds during rearing of young rabbit does compared with commercial feeds *ad libitum* (Nizza *et al.*, 1997; Xiccato *et al.*, 1999; Pereda, 2010; Martínez-Paredes, 2008) or restricted (Pascual *et al.*, 2002a; Quevedo *et al.*, 2005; Verdelhan *et al.*, 2005; Martínez-Paredes, 2008; Pereda, 2010).

Authors	Fibrous feed application	NDF[1]	First mating[2]	Lactation intake increase[3]	Reproductive performance[4]	Body condition[5]
Nizza *et al.* (1997)	50d life to 10d prepartum	34.0	--	+ 9	↑↑	--
Xiccato *et al.* (1999)	40d life to partum	40.8	↓ BW	+ 19	=	↓ losses
Pascual *et al.* (2002a)	70d life to partum	44.4	= BW	+12	↑↑	--
Quevedo *et al.* (2005)	90d life to prepartum	36.4	= BW	=	=	=
Verdelhan *et al.* (2005)	84d life to prepartum	-[6]	= ↓ BW	--	=	--
Martínez-Paredes (2008)	63d life to prepartum	47.6	= BW	+ 10	↑	=
Pereda (2010)	77d life to prepartum	50.5	= ↓ BW	=	↑	↑ (restricted) ↓ (*ad libitum*)

[1] NDF of rearing fibrous diets in % dry matter.
[2] BW situation of doe at first mating compared with control group does.
[3] Increase of intake during lactation (g DM d^{-1} $kg^{-0.75}$) compared with control group does.
[4] Improvements in reproductive performance parameters (milk, growth and/or survival, fertility…)
[5] Effect on body condition of the does.
[6] Not determined: 27% of crude fibre.

As for the effect which these diets may have on the litter performance and body condition of the doe, results are scarce but seem to be related to the maturity level of the females at first mating. Xiccato *et al.* (1999) observed that application of rearing diets makes doe rabbits reach their first effective mating with a lower BW, using greater intake during lactation, not to improve the development of the litters, but to recover the body condition disadvantage presented. However, when the does are not inseminated until they reach a suitable BW, a delay is observed in the date of the first mating, but the increase observed in the intake of the doe during lactation seems to be destined to increase their milk production (Pascual *et al.*, 2002a; Martínez-Paredes, 2008).

Recently, Martinez-Paredes *et al.* (2012), comparing different rearing systems for young rabbit does, observed that although the use of a low-energy diet during the rearing period led females to reach first mating with lower energy body reserves and lower blood leptin levels than those fed a conventional diet for reproductive does, no consequence on fertility at first AI was reported. It is well known that nutrient restriction may delay the onset of puberty, leading to the hypothesis that a critical soma must be achieved before puberty can occur (Frisch, 1980). Furthermore, although fertility rate is affected by many factors, Arias-Álvarez et al. (2009) recently proposed that reaching the permissive leptin threshold should be necessary for pubertal reproductive activity, and may be associated with inhibition of reproduction if the critical soma is insufficient to trigger gestation (Moschos et al., 2002). In fact, when the relationship between fertility and blood leptin levels of young rabbit females around first insemination is drawn (Figure 4), the hypothesis of a leptin threshold for initiation of puberty and reproductive success that is not improved by additional provision of this hormone seems to be confirmed. Consequently, these results could reveal that in terms of *ad libitum* feeding during rearing, both feed restriction and earlier use of a low-energy diet (8.7 MJ/kg DM) could lead females to achieve the critical BW and fat mass at first AI to ensure reproduction, in spite of their lower fatness and leptin content in blood.

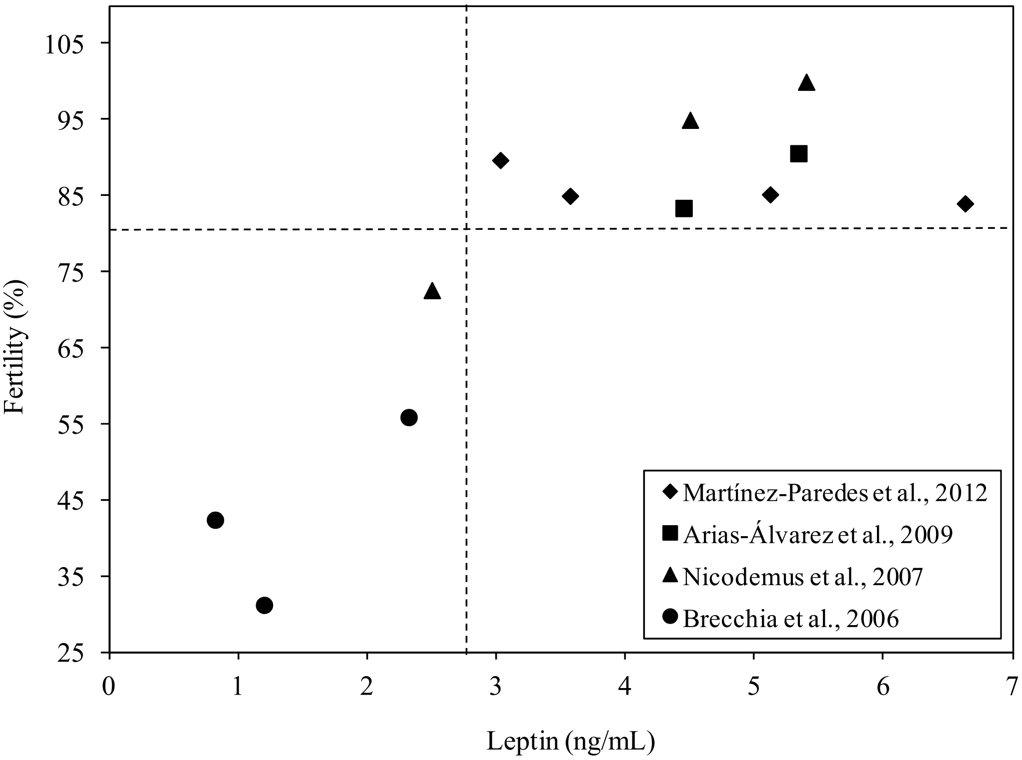


Figure 4: Relationship between leptin levels in the blood of young rabbit does at first mating (16-18 wks of age) and the fertility observed during the first reproductive cycle (Martínez-Paredes *et al.*, 2012).

On the other hand, an excessive fatness of rabbit females during rearing period has been also related high levels of plasma NEFA and glucose, and higher percentage of stillborn and culled females at first parturition (Rommers *et al.,* 2002; Martínez-Paredes *et al.*, 2012), perhaps related to a higher pregnancy toxaemia risk (Rosell, 2000).

Regarding the possible long-term effect, Nizza *et al.* (1997) indicated that the does receiving a fibrous feed during rearing presented a greater number of kits weaned during the first 4 reproductive cycles, which were also heavier. Pascual *et al.* (2002a), monitoring 46 doe rabbits over almost two years of life, observed that the values obtained for the main long-term productivity parameters (lifespan, interval between parturitions, cycles per years...) were better for the does that received fibrous diet during rearing, although without any significant differences being observed. These authors only observed a trend increasing the number of kits weaned per year by 10%. Martínez-Paredes (2008) has observed that the rearing feeding programme used did not affect the main overall productivity traits controlled in 120 reproductive rabbit does during 2 years (lifespan, fertility, kits weaned and parturitions per year…). However, the number of females culled during the first 2 cycles was half for the females receiving the fibrous diet compared with those given the commercial diet *ad libitum* during rearing. In the present congress, Savietto *et al.* (2012), in an field experiment with 619 females controlled until a minimum of 647 d (only 7% of censored records), have observed that young females reared with a fibrous diet lived on average 46.4 days more than those receiving diet for reproductive does, mainly due to the higher early survival (+4.4 and +5.1% at 1^{st} and 4^{th} parturitions), that lead to a significantly higher total production of kits per female reared (+7.4 kits born alive per female).

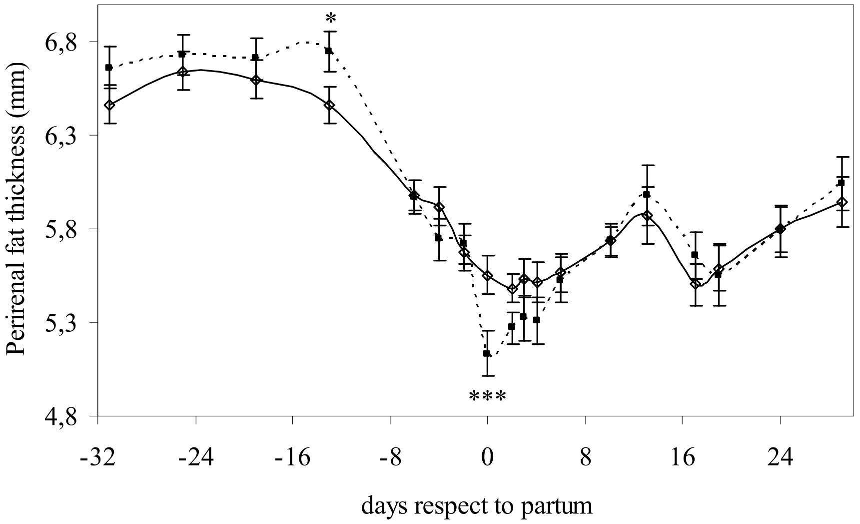
BODY CONDITION AND REPRODUCTION

As mentioned above, there is a lot of evidence of a genetic component controlling size and mobilisation of body fatness, with high priority to safeguarding body reserves of the animals (Theilgaard, 2006). Not all mobilisations are in response to environmental constraints (Friggens, 2003). In rabbits, there are also indications suggesting that the level of body reserves at a given physiological stage is highly defended. The vast majority of mammals have evolved the strategy of preparing for the forthcoming offspring by accumulating fat reserves during pregnancy (Gosling *et al.*, 1984; Chilliard, 1986, 1987; Ofteday, 2000). However, from the end of gestation onwards, an innate drive appears to decrease body fatness in favour of the current litter in spite of the nutritional resources available. Therefore, the body condition of the females will change daily during the reproductive cycle and throughout their reproductive life according to their genetically determined level. The problems will appear when the animals are forced to deviate from this adequate level, increasing susceptibility to disease, other stress factors and eventual failure (Friggens, 2003).

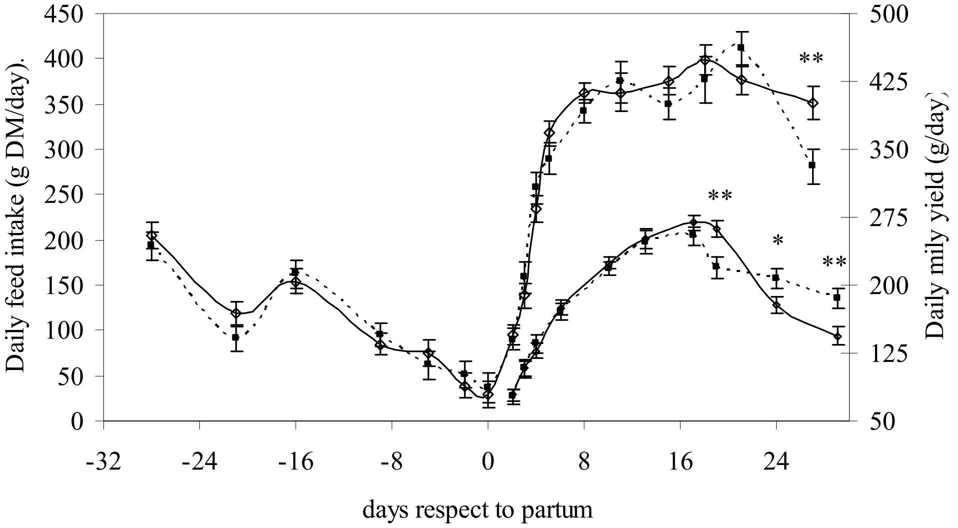
As Figures 3 and 5a show, the body condition of young rabbit females rises till the end of first pregnancy, reaching the peak 10 days before kindling. From this moment to kindling, reproductive rabbit does seem to suffer the highest body reserves mobilisation, with the body condition at parturition showing the lowest level (Savietto, 2012). This fact was recently confirmed by different works, where the evolution of body condition was controlled by different *in vivo* methods such as perirenal fat thickness (PFT; Quevedo *et al.*, 2005, 2006a; Theilggard 2006, 2009), total body electrical conductivity (TOBEC; Bolet and Fortun-Lamothe, 2002) and bioelectrical impedance analyse (BIA; Pereda, 2010). In fact, Pereda (2010) describes how the blood concentration in non-esterified fatty acids (NEFA) of primiparous rabbit does reached the higher level at partum (in average 0.9 mmol/L) in comparison to that shown at 17 weeks of age (0.22 mmol/L) and even at 21 days of lactation (0.33 mmol/L). This is mainly because rabbit foetuses show most of their growth during late pregnancy (almost doubled in the last 3 days; Moce *et al.*, 2004), while the maternal body is subject to intense catabolism (Parigi-Bini *et al.*, 1990). In fact, episodes of pregnancy toxaemia can be surmised in primiparous rabbit does, sometimes linked to *ad libitum* rearing feeding systems, which lead females to higher mobilisation of reserves in late pregnancy, higher risk of death or culling and lower litter size at birth (Rommers *et al.*, 2004a; Martínez-Paredes *et al.*, 2012).

Subsequently, body reserves are recovered during the first stage of lactation and reach a maximum around day 10 in lactation (see Figure 5a; Quevedo *et al.*, 2006b; Theilgaard *et al.*, 2006, 2009; Pereda, 2010; Savietto, 2012). Thus, rabbit females would prioritise the current offspring till kindling (devoting a great pre-partum effort), but would prioritise the next offspring immediately afterwards (promoting their quick recovery after partum). This time course of the body reserves around kindling is slightly different from other species, where the body fatness is highest just before parturition (e.g. sows: Sigfridson, 1996; dairy cows: Nielsen *et al.*, 2003), perhaps related to their different evolutionary success. For example, dairy cows usually have only one offspring per year and sows recover LH pulse only after weaning, so addressing more body reserves to the current offspring at early lactation could be expected.

However, the evolutionary success of rabbits seems to be more related to the "number" (litter size and reproduction frequency), being one of few animals with fertile acceptance at post-partum day, which could explain their early recovery of reserves. In this respect, it is worth remembering that the shapes of curves for feed intake and milk yield in rabbit does (Figure 3b) are completely different to those observed in other species (e.g. dairy cows; NRC, 1989). During the first week of lactation, the feed intake curve slope (+50 g DM per day) seems to be higher than that observed for milk yield (+30 g of milk per day), which would allow the recovery of body reserves.



(a)



(b)

Figure 5: Evolution of perirenal fat thickness, daily feed intake and daily milk yield of primiparous rabbit does effectively (◇) and non effectively (■) inseminated at 11 days post partum (* $P<0.05$; ** $P<0.01$; *** $P<0.001$). Data adapted from Savietto (2012).

Therefore, it could be hypothesised that an adequate amount of body reserves around kindling seems to be of importance in support of reproduction in rabbit females. Quevedo *et al.* (2006b) proposed that body condition of rabbit does at partum could condition the AI success at 10 days of lactation, as the greater the loss of pre-partum reserves, the greater the post-partum recovery (r = +0.29; $P<0.001$) and the lower the fertility during lactation. Savietto (2012) depicted the PFT evolution of rabbit females that were effectively and non effectively inseminated at 11 days of lactation (Figure 5) separately. Females that were not effectively inseminated presented significantly greater PFT losses in late pregnancy, lower PFT at partum and greater recovery in early lactation.

In recent decades, several works have supported the idea that rabbit does are susceptible to body energy deficit during lactation, especially the highly productive commercial hybrids whose voluntary feed and energy intake is insufficient to cover nutrient requirements for lactation and pregnancy (Xiccato, 1996; Pascual *et al.*, 2006). However, many of the studies carried out in recent years with *in vivo* technologies to control body condition call this assertion into question. Negative balances are sometimes detected during lactation, especially in primiparous rabbit does with limited voluntary feed intake (Pascual *et al.*, 2002b; Bolet and Fortun-Lamothe, 2002). Under these conditions, Pascual (2006) indicated the suitability of energy diets that clearly increased the energy intake of does in lactation (+15%; Pascual *et al.*, 1998), although energy seems to be used more to increase their productivity (Pascual *et al.*, 1999) than to recover their body condition.

However, the energy balance during lactation seems to be different in the case of multiparous rabbit does, where no relevant energy deficit seems to occur (Pascual, 2006). Furthermore, sometimes fat mobilisation during lactation was difficult to correlate with the lactation effort (reproductive rhythm, litter size, milk yield…), with no significant differences in body condition at weaning being detected in spite of the different feeding and management programmes used (Theilggard *et al.*, 2009; Pereda, 2010). In these two experiments, and regardless of the differences in body condition at partum, animals seemed to reach a similar target level of body fatness at weaning. Similar results were observed by Garnsworthy and Topps (1982) in dairy cows, where females with different levels of body fatness at calving, receiving the same feed and yielding similar amounts of milk, reached the end of the milking period with similar body condition scores. Friggens (2003) proposed as an explanation that animals were re-adjusting the size of their body reserves to optimise the cost benefit trade-off of having this safety factor (an excess of reserves is costly and a deficit of reserves is dangerous), being a possible explanation for the different energy balance behaviour observed in lactating rabbit does.

In any case, none of the negative energy balances detected for rabbit females during lactation seem to have the strength of that cited in late pregnancy. Therefore, the main risk of imbalance for reproductive rabbit does should be those programmes which would not allow recovery of the adequate soma of the female 10 days before partum, as the effort will be strong and inevitable. In fact, one of the factors conditioning the energy intake after weaning is the body condition of the female (Figure 6).

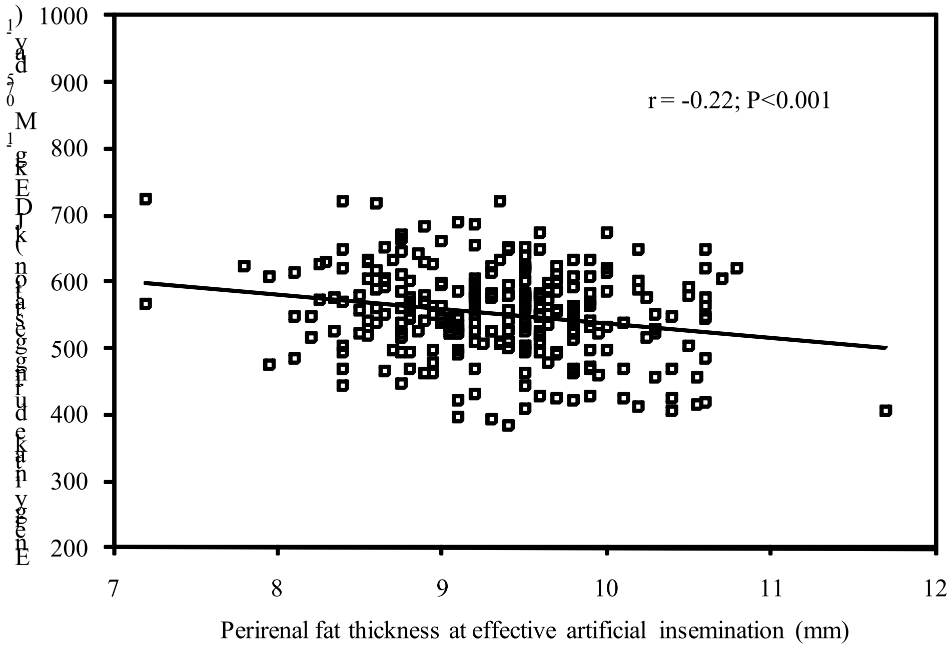


Figure 6: Relationship between the body condition of does at insemination and the energy intake during gestation of rabbit does not showing concurrence with the previous lactation (Quevedo *et al.*, 2006a).

Traditionally, concurrence of lactation and pregnancy has been associated with higher productive effort, and consequently higher body reserves mobilisation. It could be true for young reproductive rabbit does, when energy balance between parturitions is determined (Xiccato *et al.*, 1999), as concurrence reduce the weaning to next parturition period and consequently the time needed to prepare the female for the pre-partum mobilization. However, lactation-pregnancy concurrence has been frequently associated to body reserves recovery during late lactation, as pregnant rabbit does increase their priority to store reserves for the next litter, being the main consequence the reduction of milk yield (priority for the current litter).

Theilgaard *et al.* (2006) observed how the relative risk of culling was significantly ($P<0.001$) higher from weaning to kindling (7.16) than during lactation (2.44) and empty state (1.00) in reproductive rabbit does. Rosell and de la Fuente (2009), analysing the data of 366,162 females from 18 commercial farms, described the gestation stage as one of the main factors affecting mortality, with the risk of mortality per day being increased as pregnancy progressed and reaching maximum around kindling.

The evidence of the negative effect of fat reserves being too low is clear, as this may imply insufficient resources to be mobilised, but animals carrying too many fat reserves may also show a negative effect. For example, animals which are very fat at parturition have a higher risk of metabolic diseases and lower feed intake in early lactation (pigs: Revell *et al.*, 1994; Brandt *et al.*, 1999; cows: Broster and Broster, 1998; rabbits: Pascual *et al.*, 1999). Theilgaard *et al.* (2006) analysed the relative risk of reproductive rabbit does being culled on the basis of their fatness level at the maximum body condition day in lactation (Figure 7). They observed that the highest reproductive cost in terms of survival was found for the animals belonging to the lowest fatness group. This could indicate that the animals also need a certain amount of fat in early lactation to ensure enough resources to maintain the litter without loss in other body functions, such as lifespan cost. In addition, and although no significant differences were found, relative risk of being culled increased along with the fatness level. The higher risk of culling for both the highest and the lowest fatness groups suggests that there is an optimum level of fat reserves where reproduction has a lower cost, and that perhaps animal deviates from this optimum level could have negative consequences in reproduction.

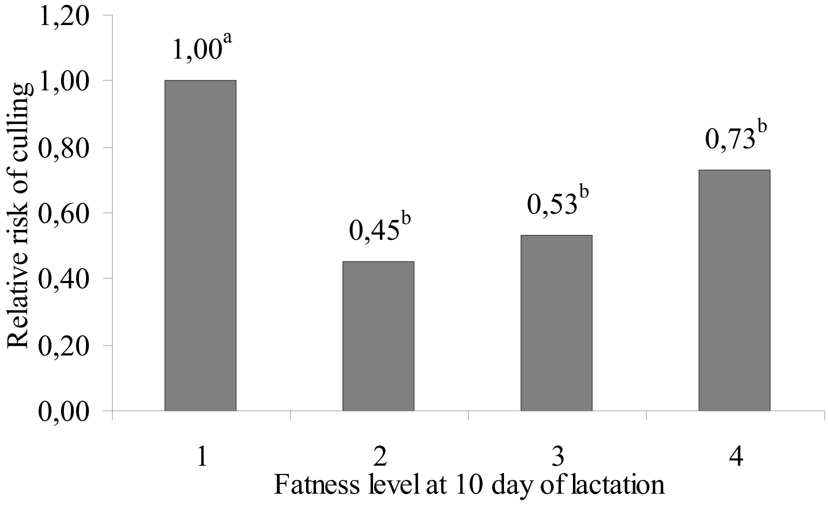


Figure 7: Relative risk estimates of being culled of reproductive does during 6 reproductive cycles in function of the fatness level (adapted from Theilgaard *et al.*, 2006).

GENETIC SELECTION AND RESOURCES ALLOCATION

Through genetic selection programmes, a considerable improvement in the productive level of our animals is being achieved. However, in some species it is frequently observed that selection by exclusively productive criteria has had some associated effects, such as lower fertility, higher rates of metabolic diseases in the animals and lower viability of their offspring (in dairy cows, Royal et al., 2002; sows, Dourmad et al., 1994; hens, Lui et al., 1995). Meat rabbits are no strangers to this phenomenon, since some selected lines present worse reproductive rates, the replacement rate of breeding females is around 110% (Rosell and de la Fuente, 2009), and one of main handicaps in rabbit production is the frequent appearance of digestive disorders in the kits after weaning (Rosell, 2003).

Selection for growth rate

One example of the possible effects of selection on reproduction is the selection for growth rate. Feed conversion ratio during the growing period is one of most important traits to be considered for genetic selection, as post-weaning feeding suppose around 40% of total production costs in rabbit farming (Baselga and Blasco, 1989). As selection for feed conversion ratio is expensive, and the expected genetic correlation with growth rate is high −0.61 to −0.68 (Lampo and Van der Broeck, 1975; Randi and Scossiroli, 1980; Moura *et al*., 1997), traditionally genetic selection programmes of paternal lines have been done in rabbits by selection for growth rate. However, recent works have highlighted that this genetic correlation seems to be lower (−0.48, even with phenotypic correlations lower than −0.20), question indirect selection (Piles *et al.*, 2004).

In any case, is well accepted that genetic groups coming from lines selected for growth rate are heavier, have greater growth rate and feed intake, and show better feed conversation ratio than those coming from lines selected for litter size (Orengo *et al.*, 2009). As consequence, animals from these paternal lines have a tendency to show higher fatness level (Larzul *et al.*, 2005; Pascual and Pla, 2007). Although there is evidence of the importance of body reserves for reproduction, an excessive fatness has also been related to negative effects on reproduction (Theilgaard *et al.*, 2006). For example, in swine, the fattest sows at mating time had fewer piglets at parturition and weaning (Tibau et al., 2003), or in dairy cattle, where females with higher fat reserves presented delayed oestrus (De Vries and Veerkamp, 2000). On the other hand, daily gain has been observed to be low or negatively associated with longevity (Theilgaard, 2006). For example, López-Serrano *et al.* (2000) obtained negative correlations between daily gain and stayability both in Large White and Landrace sows (–0.06 and –0.32, respectively), similar results of low or negative correlation were observed by Tholen *et al.* (1996) in an Australian pig population (0.02 to –0.13).

In female rabbits, it has been observed that an intermediate body fat level is optimum for fertility and that when the fat level is lower or higher than this level, it leads to a reduction in fertility of around 10-12% (Castellini *et al.,* 2006). Paternal lines selection is done according to daily weight gain in the fattening phase, and some of these lines currently present deterioration in its reproductive features, which are clearly inferior to maternal lines (Khalil and Baselga, 2002). However, estimates of genetic correlations within breeds given in the literature (Camacho and Baselga, 1990; Gomez *et al.*, 1998; Garreau *et al.*, 2000; García and Baselga, 2002a; Piles and Tusell, 2011) among litter size or fertility and growth traits are low or zero.

Main of these paternal lines are addressed to AI, and the most recent results associate a possible increase in abnormal spermatozoa and a high risk of fertility problems with the increase in weight of the breeding bucks (Du Plessis *et al.*, 2010). On the other hand, individuals with higher weight present a drop in androgen levels and high levels of oestrogens (Hammoud *et al.*, 2008), and obesity affects the GnRH-LH-FSH pulses, altering Leydig and Sertoli cell functions, and in turn modifying sperm maturation (Bélanger *et al.*, 2002). These modifications in the hormone profiles could explain the increased risk of altering the seminal parameters in males as their weight increases (Hammoud *et al.*, 2008).

These controversial results reveal the importance of further scientific effort about the possible effect of selection for growth rate on resources allocation, and the possible effect on reproduction and lifespan, as well as on the genetic relationships of growth rate and reproduction (Garreau *et al.*, 2004).

Selection for litter size

From the above proposed deductions for body condition and reproduction relationship, it could be expected that selection for improved litter size (reproduction), frequently used in rabbits (García and Baselga, 2002a, 2002b; Tudela *et al.*, 2003), should have changed the ability of rabbit females to obtain resources. On the contrary, negative consequences on body condition and survival should be expected.

Using freezing and transfer techniques (García-Ximénez *et al.*, 1996), Quevedo *et al.* (2005 and 2006b) have studied the effect of selection for litter size at weaning on the performance and physiological and productive characteristics of the rabbit does by the contemporary comparison of crossbred does with 12 generations of differential selection (Table 3). As mentioned above, current females presented a greater number of live-born kits (+1.1 kits) than older ones. However, when these females are subjected to the same productive pressure (standardised litter), differences in feed intake and milk production are observed at the onset of lactation in favour of the animals selected more for litter size. These results could explain a possible change in the use of available resources by the animal as a result of the selection. In this way, when selecting the animals by litter size at weaning, we would be selecting both prolificacy (and in fact more kits are born) and maternal aptitude criteria (survival of the kits). Survival in lactation is mainly determined by what happens in the first days after parturition, and is clearly related to the ingestion of energy by the kits in that period, which is why the increase in milk production as a result of the greater ingestion of the does would be favourable.

Table 3: Effect of selection for litter size at weaning on reproductive does and their litters (adapted from Quevedo *et al.*, 2006b).

Type of females		Old	Current
Nº born alive:	Primiparous	8.31^{a}	10.76^{b}
	Multiparous	9.18	9.90
Intake (g DM kg$^{-0.75}$ d^{-1}):	0-21d lactation	113^{a}	117^{b}
	21-28d lactation	112	112
Milk production (g d^{-1}):	0-7d lactation	156^{a}	165^{b}
	8-28d lactation	215	218

^{a,b} Measures without letters in common are significantly different to P<0.05.

Mammals have evolved a breeding strategy where they fuel their reproduction from energy gained earlier and stored in body reserves. The body reserves are subsequently used to sustain the reproduction cycle, usually at the time of greatest energy demand, e.g. to ensure foetal growth at late pregnancy or nursing in the form of milk for the litter at early lactation. Selection experiments show evidence for a relationship between reproduction and body reserves as selection for prolificacy increases the demand of energy to the litter; selection for litter size therefore increases body fatness (*e.g.* pigs: Holl and Robinson, 2003; Estany *et al.*, 2002). In fact, Quevedo *et al.* (2005) demonstrated a possible increase in the efficacy of use of energy feed for foetus growth as a consequence of selection by reproduction criteria (0.29 and 0.33 for old and current does, respectively), as the product of pregnancy was clearly higher in the selected does, despite not showing a greater energy ingestion, nor a greater mobilisation of reserves. In addition, Quevedo *et al.* (2006b) observed that more selected animals for litter size presented a greater PFT at 10th day of lactation (+0.12±0.06 mm; $P<0.05$), considered as the maximum body condition day. Thus, it could be that the selection of the animals by reproductive criteria has produced a response correlated in the capacity of the animals to obtain resources (van Noordwijk and de Jong, 1986; Reznick *et al.*, 2002).

Similar results have been recently obtained recently by Savietto (2012), where more selected rabbit females (plus 20 generations of selection for litter size at weaning), under conditions of unlimited resources, presented a significantly higher daily feed intake and milk yield at the first week of lactation, and a lower milk yield at the last week of lactation. Friggens (2003) proposed that maternal investments for the current litter reach to the maximum around parturition in order to contribute to the viability of the newborn litter (Figure 8). Selection for litter size at weaning could have affected the relative priority for the current litter flattening the shape around kindling to ensure an adequate development of larger but probably less mature litters. Increasing priority for the actual litter at the end of pregnancy leads to an extra effort to ensure an adequate foetal development, which could be related with the higher reduction in the lactation effort observed at the end of lactation in the previous reproductive cycle, and of the high mobilisation observed at the end of pregnancy in this specie (Savietto, 2012). In addition, the flattening of the priority shape would allow a greater maternal investment after parturition (higher milk yield) as kit survival index is mainly determined by what happens at early life, being clearly related with the energy intake of kits during these days (Quevedo *et al.*, 2006b). After that, priority for the current litter would be reduced, as producing milk in excess of that required for the litter –when it becomes progressively less depend on mothers milk– will not improve the litter's chances of survival.

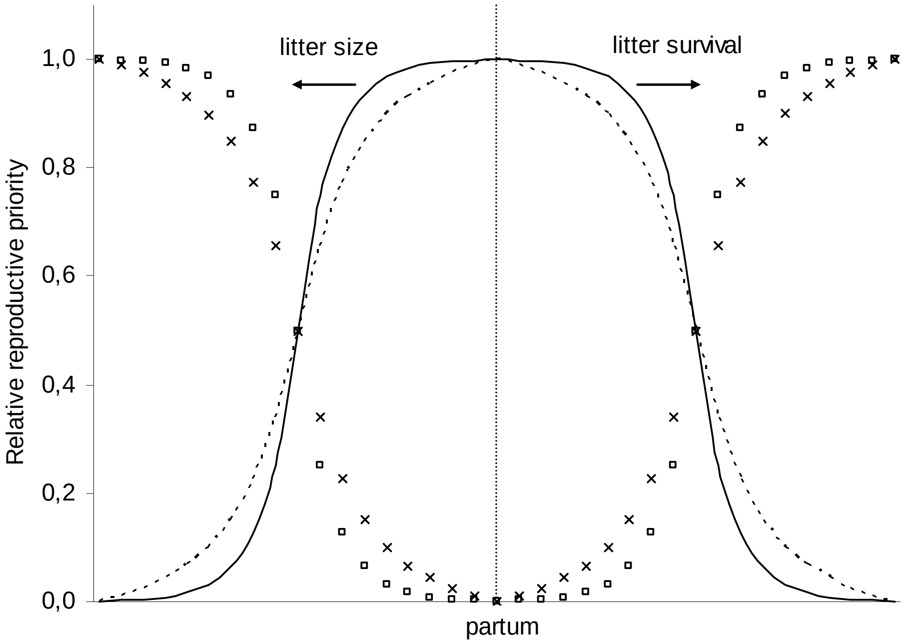


Figure 8: Proposal of Savietto (2012) for the evolution of the relative reproductive priority for the current [less (······) and more (——) selected for litter size] and the future litter [less (× × ×) and more (□□□) selected for litter size] on rabbit females from conception to weaning. The priority accorded the current litter is assumed to be the maternal investment rate scaled from 0 to 1 as proposed Friggens (2003).

Therefore, when prolific animals are selected for reproduction, it seems to be enhanced those characteristics of the animal that ensure their selection success, that we could call as "the number", such as prolificacy and the ability to manage more appropriately the resources when they are not limited to ensure the viability of their larger litter but without negative effects to the future one.

However, under a nutritional restricted environment, Savietto (2012) observed how more selected animals for litter size at weaning showed a higher delay in adjusting their feed intake to compensate low dietary DE content, which also led to a lower milk yield. In the opposite, main of the female body traits controlled were less affected by the feeding restriction in more selected animals. These results seems to indicate that selection for litter size could increase the sensibility of animals to this type of environmental challenge, which led to a change on nutrient partitioning to reduce the performance under this situation of restriction.

But, why selection for litter size lead to more environmentally sensible animals? As it was proposed above, the fitness characteristics enhanced under this selection criterion is "the number". When the resources available are limited at the present, the success of the actual litter could be questioned, so the animal probably decide to reduce the priority for the actual litter (relatively addressing lower amount of resources to those traits directly related to the actual litter performance, as energy intake and milk yield), while seems to be prioritized the next litter (relatively increasing the fuel for the future litter, the body reserves). Therefore, when animals are selected for reproductive traits as litter size and the resources available are limited at the present, so as they can't ensure the success of the actual litter, maternal investment for the actual litter is reduced (and as a consequence animals are less robust –or more sensible to the environment–) to concentrate their efforts to ensure the next one (Friggens, 2003) when perhaps resources and environment would be improved.

Selection for longevity

Longevity reflects the animal's ability not to be culled or die. The main culling reasons in animal production include diseases, low fertility and low production (Vollema, 1998). During recent decades there has been a considerable rise in livestock production per animal. This increase is largely due to successful selection for productive traits (*e.g.* milk yield, growth, litter size) in combination with an improved dietary formulation and management. Focus almost exclusively on production traits has had some associated negative side effects such as lower fertility, higher frequency of metabolic diseases for the animal and lower viability of the offspring. However, positive relationships between productive traits and longevity are also still frequently reported (Lynch and Walsh, 1998). So, it is still not clear when to expect positive or negative relationships between production, reproduction and survival.

In rabbit production, the main traits of interest are growth rate, litter size and fertility. Selection for reproduction performance has so far not been reported to have negative consequences on longevity. For example, it was reported that high litter sizes was positively associated with longevity in meat type does (Garreau *et al.*, 2001; Sánchez *et al.*, 2006). Also, in an experiment comparing a rabbit line selected for litter size during seven generations with a control line did not find any difference in longevity (Rinaldo and Bolet, 1988). The only work in rabbit production estimating the genetic correlation between reproductive performance and survival found that this correlation was no different from zero (Sánchez *et al*., 2006).

Recently, Theilgaard *et al.* (2007) evaluated genetic differences in reproductive performance and body condition traits during successive parities between a longevous productive (LP) line [constituted by hyper selection of animals having an extremely high number of parities (at least 25) and an average reproductive performance] compared to a line (V) selected for 31 generations for litter size at weaning]. Both lines were found to have an equal reproductive performance in the first three cycles but when animals were subjected to a no-programmed restricted environment (change of nutritional management to feed restriction after weaning) in one of the farms from the third reproductive cycle, litter size at birth of V line females was depleted from this moment while those of the LP line maintained their prolificacy at the expense of a reduction of their greater soma (Figure 9). Theilgaard *et al.* (2007) hypothesized that the higher body soma of adult LP females (+250 g than adult V females) allows them a greater body buffer capacity reducing their environmental sensitivity.

Therefore, hyper selection for reproductive longevity and average prolificacy could delay reproductive senescence, as this newly founded line seems to show less environmental sensitivity. Nevertheless, no indication of a trade-off between reproduction and survival was found in these experiments in any case. When sufficient resources are provided, the female should be better able to meet the demands of both reproduction and maintenance without compromising either. Failure to provide enough energy for maintenance will have a deteriorative effect on her physiological condition, and continued reproduction under such conditions will likely increase the susceptibility to disease and other stress factors (Friggens, 2003). So, these animals might be less robust and show an increased susceptibility to disease, other stress factors and eventual failure.

In rabbits, Theilgaard *et al.* (2007) observed that the LP line was heavier than the V line (4.27 *vs.* 4.12 kg; $P<0.05$) throughout 6 reproductive cycles, in agreement with experiments where selecting for reproductive longevity in mice (Nagai *et al.,* 1995) and on late reproduction in flies (Partridge and Fowler, 1992) also increased BW, suggesting that selection for longer life favours extended growth to produce a more durable adult soma.

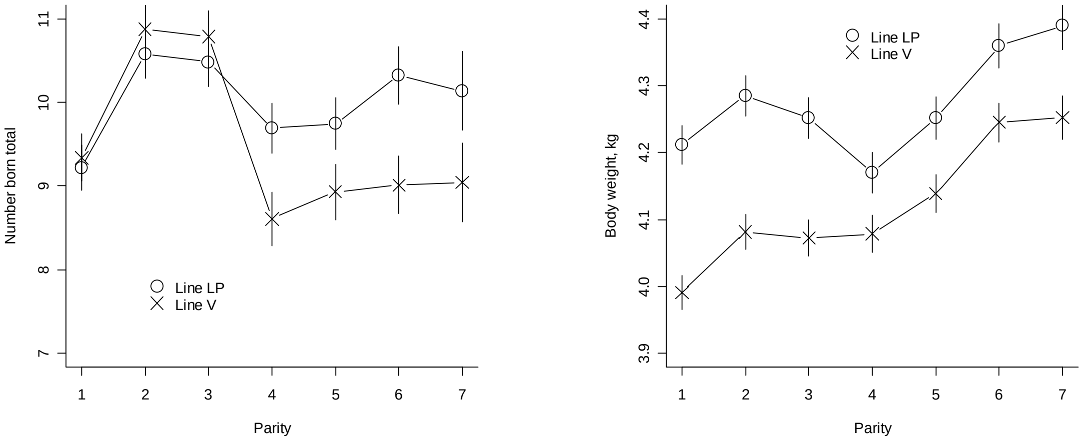


Figure 9: Effect of genetic line on the evolution of the number of total born and acceptance rate (adapted from Theilgaard *et al.*, 2007).

To confirm these results, Theilgaard *et al.* (2009) compared the performance and body condition traits of LP and V does, subjected to different productive effort levels (previous AI at partum or weaning, and litter sizes of 5 or 9 pups) during their second lactation. LP does were again significantly heavier than the V line, but also showed a better body condition (+0.50±0.09 mm of PFT; $P<0.05$) and a lower mobilisation (-0.11±0.03 mmol of NEFA/L; $P<0.05$) at the beginning of lactation, confirming the greater soma of this type of animals to confront productive and environmental challenges. In fact, LP does showed a greater milk yield than V does, even per kg of metabolic weight ($+5\pm2$ g kg^{-1} $BW^{0.75}$ day^{-1}; $P<0.05$), and especially when lactation pressure increased (9 pups).

This greater soma of rabbit females selected for reproductive longevity seems to allow them to better cope with the possible productive challenges that they could meet in the course of their productive life. They seem to present a greater plasticity, enabling them to use their greater soma to overcome these demanding situations, reflected in the fact that the greater the productive effort, the lower the differences observed in BW between lines. Therefore, rabbit females selected for reproductive longevity are more “robust” in these situations (more milk for the offspring), and their risk of early culling for low productivity is consequently reduced.

Robustness

It seems that when resources availability is not limited, more selected animals can successfully cope most of their higher needs without too much negative consequences. In fact, it’s not strange to find even positive relationships between productive traits and survival for reproductive stock when animals were reared under controlled environment, *i.e* for cows (Short and Lawlor, 1992), sows (Serenius and Stalder, 2004) and rabbit does (Theilgaard *et al.*, 2006). However, it’s when animals suffer punctual but no infrequent and even cyclical suboptimal environments (*i.e.* resources limitation, heat stress, immunological challenge), when the more sensitivity of high producing animals to these stressing conditions appears (Schinkel *et al.*, 1999; De Greef *et al.*, 2001; Yalcin *et al.*, 2001; Windig *et al.*, 2005).

Knap (2005) defined the concept of robustness in farm animal as ‘the ability to combine a high production potential with resilience to stressors, allowing for unproblematic expression of a high production potential in a wide variety of environmental conditions’. From the results discussed above, it could be hypothesized that perhaps selection in rabbits for only reproductive criteria could have affected the ability of the animals to maintain their reproductive level under stressing environments, while the inclusion of longevity criteria in the constitution of the line could have contributed to increase their robustness.

With this aim, Savietto (2012) has recently evaluated how selection for litter size at weaning (line V) or the foundation for reproductive longevity criteria (LP line) could have affected the ability of animals to confront restricted resources conditions, by the use of a low-energy diet, during their first two reproductive cycles. The results of this work shows how, when resources were limited, LP females compensate the lower dietary energy with a higher daily feed intake even at the first lactation, while daily energy intake of V females was significantly lower to that observed under no-limiting conditions. So, LP females where able to maintain unaffected their milk yield, litter growth and body condition, as well as the litter size at the second kindling, while V36 females reduced their milk yield trying to maintain their body condition and next litter size. During the second lactation, LP females had a lower milk yield to that observed under no-limiting conditions but without any negative effect on their body condition and on the litter performance at third birth, while V36 females on restricted conditions presented a continuous worsening of their main performance traits (milk yield and body condition), being clearly affected the size of their litters at the third kindling (–1.8 and –2.6 total and alive kits born, respectively; $P<0.05$).

For a better picture of environment sensibility, in the Figure 10 is represented, by means of response graphics, the effect of genotype (V or LP) on dietary energy intake, body reserves and kits born alive in function of the dietary energy (normal or restricted). As can be seen, the response to environment restriction of females coming from a line founded for reproductive longevity criteria was flatter than those obtained for females selected for litter size at weaning in all the traits controlled, highlighting their differences on robustness. Under no-limiting conditions, females selected for reproduction show their superiority in prolificacy, but when environment quality decreases this animals showed higher reduction in their ability to obtain resources, maintenance of body reserves and reproductive performance.

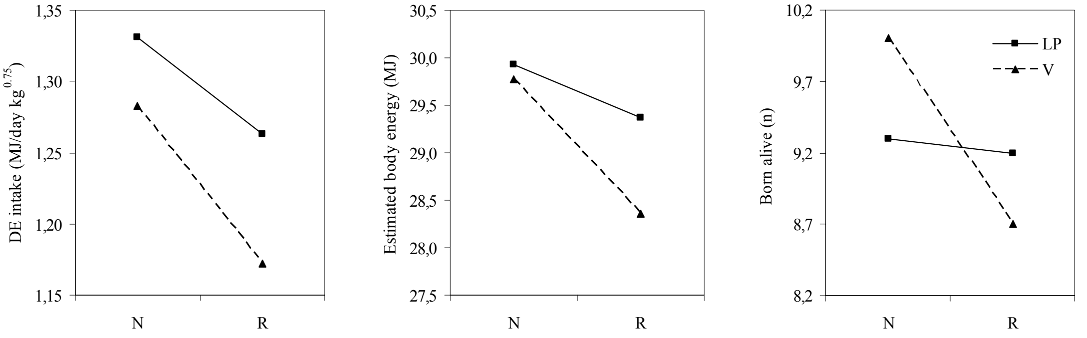


Figure 10: Effect of genetic type (■ LP and ▲ V) on average estimated body energy, digestible energy (DE) intake and number of kits born alive (second and third kindling) in function of the dietary environment [normal (N) *vs.* restricted (R)].

In other species has been also observed signs of reduced robustness in highly productive stocks (Rauw *et al.*, 1998; Knap and Rauw, 2009; Siegel *et al.*, 2009; Veerkamp *et al.*, 2009), supported by the resource allocation theory (Beilharz, 1998; Glazier, 2009) – the energetic resources of an individual are limited and their allocation across metabolic functions is optimized towards the best adaptation of the individual to its environment (fitness). Therefore, when we genetically select for reproduction traits logically resources could be redirected towards those reproduction traits at the expense of other traits (such as robustness traits), which leads to genotype×environment interaction. However, resources allocations theory also consider the possible development by the animals of nutrient partitioning strategies, which allow to obtain additional resources to optimized reproduction without robustness penalty or to optimize resources allocation thought time to ensure their fitness success.

These results highlight the improvement on robustness characteristics when rabbits are selected or founded for reproductive longevity criteria. These criteria would give additional tools to the animals, for a more appropriately management of the available resources under conditions of high productive effort (Theilgaard *et al.*, 2009) and/or nutritional challenge. Therefore, while animals selected for reproduction clearly seem to be more sensible to the nutritional challenge, robust females were able to maintain main of their reproduction traits unaffected, which could contribute to confer their reproductive longevous character.

Other component in the definition of the lifespan of the female is her sensitivity to the common diseases that could appear on the rabbit farms. Possible changes in resources allocation, consequence of genetic selection or reproductive management, should lead female to situations where body condition could be withdrawn from the adequate level increasing the susceptibility of animals to punctual immunological challenges. For example, the greatest drop in body reserves takes place at the end of gestation, that is the time of greater elimination of commercial does on the farm (Rosell and de la Fuente, 2009) and lowest B lymphocytes counts in blood (Ferrian *et al.*, 2012), and an excessive fall-off of the reserves at parturition conditions the success of mating during the following lactation (Quevedo, 2005; Savietto, 2012). These results would reflect the importance of not moving too far from the appropriate body status to ensure reproduction and reduce the risk of elimination. Thus, Guerrero *et al.* (2010) and Ferrian *et al.* (2012) observed that there is a positive correlation between the body status of the rabbit does and the population of B lymphocytes (from +0.40 to +0.82), and that there is a positive correlation between the lymphocyte populations of the does and their litters (*e.g.* T CD5+: +0.35). Besides, there is a maternal effect on the definition of the digestive microbiota of the kits (Abecia *et al.,* 2007), and a litter (and/or maternal) effect on the rate of digestive disorders in growing rabbits (Quevedo *et al*., 2003; Carabaño *et al*., 2006).

In other species there is evidence that sensitivity to immune challenges may be different depending on the genetic diversity (Rauw *et al*., 1998; Siegel and Honaker, 2009). There, it is possible that this “more robust” type of animals may also have a greater capacity to withstand immune challenges, and that the introduction of this type of animals could improve the general health conditions on the farm. In rabbit does, Ferrian *et al.* (2012) has recently reported how selection for litter size during 20 generations could have reduced the average counts of total and B Lymphocytes in blood (−17 and −36%, respectively; $P<0.05$), mainly due to the decrease of this populations in the blood of more selected females from the first to the second parturition. In addition, this work also reported an increase in the lymphocytes counts (total and T CD5+) of “more robust” females under heat respect to normal conditions when lymphocytes populations showed the lowest value (second parturition), while “less robust” females counts remained invariable. Other recent works (Savietto *et al.*, 2011; Ferrian, 2012) would show indications in favor of the theory about a possible improvement of the immune system modulation in robust animals (lower sensitivity to challenge with LPS, or lower mortality of their kits during the fattening period), although further research effort must be done in the future to confirm this matter.

CONCLUSIONS

Along the present revision has been provided enough evidence about how nutrient partitioning between the different metabolic functions throughout rabbit female life is genetically driven. Consequently, resources allocation in the rabbit female is done to ensure their genetic selection success at every moment. Therefore, if rabbit females has been selected by a reproduction criteria, as litter size at weaning, nutrient partitioning is defined as the optimal trade-off between the maternal investment addressed to the current and the future litter, to maximise the number of viable litters produce in a lifetime. On the other hand, the constitution of a line through high selection intensity in its foundation by reproductive longevity has lead to obtain rabbit females characterised by a higher robustness. Particular nutrient partitioning in these robust females enables them to better cope with the possible reproductive, environmental and immunological challenges that they may meet in the course of their productive life, which could explain their great life expectancy on the farm.

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