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RESOURCES ALLOCATION IN REPRODUCTIVE RABBIT DOES: A REVIEW OF FEEDING AND GENETIC STRATEGIES FOR SUITABLE PERFORMANCE

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Abstract: This article reviews how frequent feeding and selection programmes can affect resource allocation in rabbit does during reproduction. The consequences of these programmes and the central role of body condition for suitable female performance are analysed considering genetic level, health and welfare. Future reproductive potential of reproductive rabbit females is decided before first partum. There is 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 as the last of the 'pure' data on the animal, a sign of the animal soma that is probably related to its productive potential. An adequate feeding system during rearing and first pregnancy is relevant for the reproductive performance of rabbit females in the short and long term. The body condition of females changes during the reproductive cycle and throughout their reproductive life according to their genetically determined level. The problems arise when the animals are forced to diverge from this appropriate level, increasing susceptibility to disease, other stress factors and eventual failure. Negative energy balances detected during lactation do not seem to have the strength of those observed in late pregnancy. Genetic selection for litter size at weaning has increased prolificacy, but also the ability to obtain resources without compromising the survival of rabbit females. However, it could also have increased the susceptibility of animals to the environment, focusing more on the maternal investment in the future litter rather than on the current one under restricted conditions to maximise their fitness. Rabbit does selected for reproductive longevity have a greater soma, which enables them to better cope with the possible productive challenges. There is also evidence that they have greater plasticity in using their soma, making them more robust to overcome demanding situations. In addition, there is evidence of a possible improvement of immune system modulation in such robust animals.

Key Words: 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 that of other intensively farmed animals such as pigs, with similar on-farm mortality risk (Lebas, 2000; Rosell and de la Fuente, 2009). However, the outbreak of any new challenge affecting minor species, such as epizootic rabbit enteropathy (ERE), usually requires great scientific effort to reduce the economic impact. For example, many works have studied the influence of nutrition on intestinal health of growing rabbits, recently reported in acknowledged revisions (Gidenne and Garcia, 2006; Carabaño *et al.*, 2008, 2009).

In any case, these efforts should not divert us from the study of current breeding systems for reproductive rabbit does, which may unbalance nutrient partitioning and affect global farm health and welfare and their possible implication in the incidence of specific illnesses. In the last 2 decades, we have moved on from more or less traditional production systems to more intensive ones using new prolific lines with an adjustment of their nutritional requirements to the new demands (Maertens, 1992). Although 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/d per generation of selection (Baselga, 2004)– it is equally true that the reproductive does have suffered to a greater extent the effects of these improvements and new production systems.

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. Moreover, 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 5000 kits from 5 reproductive cycles, described an increase in mortality during the growing period with the mother's age (from 5 to 29%), being 22% of females responsible for 50% of the mortality. In fact, García *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 appropriate genetic selection programmes. The present review examines how frequent feeding and selection programmes may affect the allocation of resources in reproductive rabbit does and the possible consequences resulted from these changes, as well as the central role of body condition for suitable female performance considering genetic level, health and welfare.

NUTRIENT PARTITIONING

The different metabolic functions of a rabbit female (growth, gestation, milk production, health…) must be covered from the available resources (food or body reserves). The process whereby available nutrients are channelled in varying proportions to these functions is known as nutrient partitioning (Friggens and Newbold, 2007). Nutrient partitioning changes depending on 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 the relative priorities for the different life functions vary throughout the doe's life (Martin and Sauvant, 2010). Thus, it is widely accepted that resource 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 is 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 was 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 voluntary feed intake as their growth is not completed, which could lead to mobilisation of body reserves during lactation (Xiccato, 1996; Pascual *et al*., 2003; Fortun-Lamothe, 2006). However, there is no relevant relationship between body weight

(BW) and daily feed intake during the first lactation (Figure 1) as primiparous does with a 1 kg difference in BW present a similar feed intake.

If we accept that there is a genetic component driving temporal changes in body reserves, the occasional negative energy balance occurring in rabbit females should not be considered a malfunction in the animal, but a natural adaptation designed to maximise the chances of evolutionary success (Friggens and Newbold, 2007). From an evolutionary point of view, rabbit selection has focused on maximising the number of viable litters produced in a lifetime. To achieve this goal, the optimum trade-off between number of pregnancies and postnatal investment in litter viability must be defined (Friggens, 2003), i.e. the optimal trade-off between the maternal investment addressed to the current and future litters.
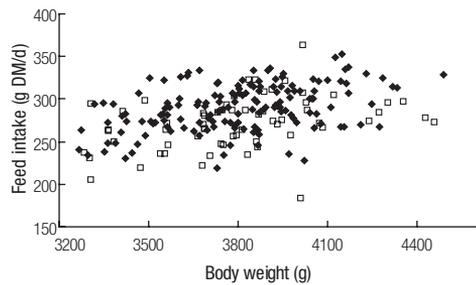

Figure 1: Relationship between dry matter intake (g DM/d) and body weight (g) of primiparous rabbit does (data from □ Pascual *et al.*, 2002b and ◆ Quevedo *et al.*, 2006b).

Whether the female rabbit becomes pregnant or not is usually highly dependent upon the resources available, which could also be assisted by hormonal and bio-stimulation methods (Theau-Clément, 2007). However, the female does not know what the future available resources will be when the reproduction effort is increased (end of pregnancy and onset of lactation). Thus, the pregnant doe stores reserves for the forthcoming litter (similar to other mammals; Oftedal, 2000), as resources available for foetal growth and early suckling will clearly affect the litter's chances of survival. Body reserve mobilisation observed around parturition is mainly addressed to this task (Savietto, 2013) and seems to be independent of the resources available at that point. In fact, the additional fat build-up, necessary for the transfer of energy to the litter via milk supply and to maintain a heavier soma, is energetically costly, reduces mobility, and increases the risk of being predated (McNamara and Houston, 1990). Moreover, yielding more milk than that required at the end of lactation will not improve the litter's chances of survival. Therefore, milk yield is decreased as the priority of restoring reserves for the future litter starts to increase.

Given these considerations, under non-limiting resource conditions, the traditional view of body reserves mobilisation in rabbit does as a response to feed intake must give way to an animal viewpoint, where feed intake should be considered more as an "output" resulting from the allocation of resources in the female to ensure current and future litter viability. This new view is applied in the present work to assess how rearing, feeding and genetic selection programmes could affect both body conditioning and nutrient partitioning, and their possible effect on reproduction and lifespan.

YOUNG RABBIT FEMALES

As expected, many works have addressed the appropriate 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 programming their future reproductive performance, health and lifespan. Among these crucial milestones, here we highlight the birth weight, maturity of the female at first mating and the rearing feeding programme used.

Birth weight

There is sufficient evidence of the negative consequences of deficient foetal nutrition on adult reproductive performance (McEvoy and Robinson, 2003). In sheep, Gunn *et al.* (1995) observed that undernutrition in either foetal or early life reduced adult reproductive performance. 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 early undernutrition arises as a result of the greater competition for nutrients during gestation (number of foetus, position in the uterus, 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 Szendrő, 1990; Poigner *et al.*, 2000; Szendrő *et al.*, 2006; Martínez-Paredes *et al.*, 2009; Savietto *et al.*, 2010) 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 young animals were reared (Poigner *et al.*, 2000; Martínez-Paredes *et al.*, 2009; Savietto *et al.*, 2010), although both the amount of milk and feed received during their rearing significantly affected their performance at the age of the first mating (Rommers *et al.*, 2001; Szendrő *et al.*, 2006). Recently, Savietto *et al.* (2010) proposed a possible threshold for the birth weight of females that allows them to reach the beginning of their reproductive life in a suitable body condition, which could maximise their future reproductive potential (Figure 2).
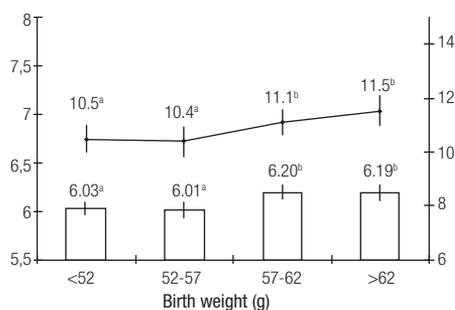
Figure 2: Effect of birth weight of females on their perirenal fat thickness (mm) at first mating (bars; left axis) and litter size at birth (total born) in their two first litters (lines; right axis) (Savietto *et al.*, 2010). [ab]Bars or points not sharing superscript are different at $P<0.05$.
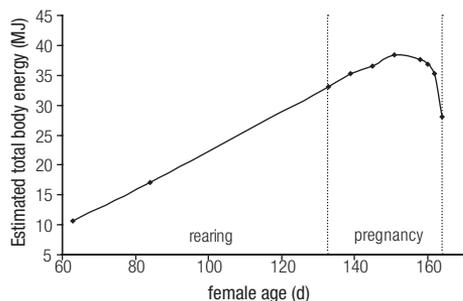
Figure 3: Evolution of the estimated total body energy of young rabbit females during the rearing period and first pregnancy (drawn using own data).

Similarly, 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 with the highest percentage of sperm abnormalities ($P<0.05$).

The possible disadvantage of reduced birth weight in the subsequent reproductive potential of the females should be considered in the new genetic selection programmes for multiparous species. Unfavourable genetic correlation has been 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 increases litter weight at birth but reduces the individual birth weight (Moce and Santacreu, 2010), may cause 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 a phenotypic correlation between litter size and the within-litter variability in birth weight.

Maturity at first mating

As shown in Figure 3, the total body energy of the young rabbit female increases linearly from 9 wk of age to the end of 1st pregnancy, when a clear drop occurs until the first parturition (Parigi-Bini *et al.*, 1990;

Pascual, personal communication). However, this graph represents the average of several females, with the body energy trajectory showing a great variability in terms of the animal (genetic effects), feeding programme, and age at first mating.

The moment of first mating has frequently been identified as a crucial point in development of the young females. This is the last item of 'pure' data on the animal, a sign of the animal soma that is probably related to their productive potential. From this moment on, all their productive 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 at first mating deviates from the 'optimum level' there are negative consequences on reproduction. O'Downd *et al.* (1997) observed how those nutritional strategies that increased body fat reserves in genetically lean young breeding sows improved their fertility and productive lifespan. Referring to a fat swine line, Tarrés *et al.* (2006) proposed the existence of an optimal female body condition at first farrowing to maximise longevity. They recommended that backfat thickness should be more than 16 mm at the end of the rearing period and that this level should be maintained until the first parturition without exceeding 19 mm. In fact, an excessive fatness at first mating has also been related to reduced longevity, with moderate feeding restriction being recommended during the rearing period of gilts (Jørgensen and Sørensen, 1998). In other studies, however, gilt backfat obtained from field testing performed before first parturition did not have any effect on reproductive life (Yazdi *et al.*, 2000a), but showed positive phenotypic (Yazdi *et al.*, 2000b) and genetic effects (López-Serrano *et al.*, 2000).

Similar results have been found for young rabbit females. Quevedo *et al.* (2005) compared 2 types of crossbreed rabbit does obtained from the cross of different generations of the same 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 3 mo of age, although differences between animals disappeared thereafter. As expected, the selection for prolificacy resulted in increased litter sizes at birth of the contemporary generation (Quevedo *et al.*, 2005 and 2006a) compared with the old one (+1.1 total kits born on av.; $P<0.05$). For these same animals, Theilgaard *et al.* (2006) reported that although no significant effect of selection for litter size at weaning on reproductive lifespan was observed, there was a tendency towards longer survival in the contemporary population (Table 1). This result is at least surprising, since resource allocation theories explain that higher reproduction has an antagonistic effect on longevity, as more resources are directed toward reproduction and consequently less are available for the longevity (Kirkwood and Austad, 2000; Mysterud *et al.*, 2002). Thus, the trend for higher longevity in the current population with the highest reproductive potential could mean that selection for litter size has not only increased the genetic level for this trait but may also have altered the ability to acquire resources (Van Noordwijk and de Jong, 1986; Reznick *et al.*, 2002). The higher body condition at the beginning of their reproductive life could be an indicator of this ability.

Other works done with young rabbit females have provided evidence of the relevant role of body fatness at the onset of reproductive life in mediating the trade-offs between reproduction and longevity. Rommers *et al.* (2002) observed how heavier rabbit females at 14.5 wk 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 maturity level of young rabbit females

Table 1: Effect of selection for litter size at weaning on the body condition of young rabbit females and their subsequent reproductive performance and culling risk during 5 reproductive cycles (adapted from 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 mo 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 culling risk[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 at $P<0.05$.

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/d) until the first kindling, to avoid overconditioning, high perinatal mortality, possible decrease in voluntary consumption at the onset of lactation and reduction of expected lifespan (Partridge, 1986; Maertens, 1992). However, some recent works show that restriction during rearing can lead to a reduction in female maturity at the first insemination (Rommers *et al.*, 2004b). The insemination of animals with lower BW has been related to lower fertility (Szendrő *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 successive cycles. From these data, it seems that the BW, body condition and age of young rabbit females at first mating can be very important to avoid the above cited problems, independently of the feeding programme used.

An alternative to restriction can be the use of fibrous feed *ad libitum* which, besides avoiding an excessive fattening of the does at first parturition, may 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 shown in Table 2, several works have examined the possibility of stimulating feed intake of reproductive does during the first lactations by the inclusion of fibrous feeds administered *ad libitum* during the rearing period, but different results have been obtained depending on the feed used and the moment of its application.

From these works, it can be deduced that the inclusion of fibrous diets during rearing should take place as soon as possible and not much beyond 60-70 d of life. When the fibrous diet is included later to avoid a delay in the growth of young does, it does not affect the development of the digestive tract in the same way and no effects are observed in the productivity of reproductive does (Quevedo *et al.*, 2005; Verdelhan *et al.*, 2005). On the other hand, the largest increases in female intake during lactation (+11 to +18%) were observed with 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)	50 d life to 10 d prepartum	34.0	--	+9	↑↑	--
Xiccato *et al.* (1999)	40 d life to partum	40.8	↓BW	+19	=	↓losses
Pascual *et al.* (2002a)	70 d life to partum	44.4	= BW	+12	↑↑	--
Quevedo *et al.* (2005)	90 d life to prepartum	36.4	= BW	=	=	=
Verdelhan *et al.* (2005)	84 d life to prepartum	-[6]	=↓BW	--	=	--
Martínez-Paredes (2008)	63 d life to prepartum	47.6	= BW	+10		=
Pereda (2010)	77 d life to prepartum	50.5	=↓BW	=	↑	↑(restricted) ↓(*ad libitum*)

[1] Neutral detergent fibre of rearing fibrous diets in % dry matter.

[2] Body weight (BW) situation of doe at first mating compared with control group does: ↓lower, = similar.

[3] Increase of feed intake during lactation (g DM d^{-1} kg$^{-0.75}$) respect to control: = similar.

[4] Improvements in reproductive performance parameters (milk, growth and/or survival, fertility…):↑↑ high, ↑ normal, = no effect.

[5] Effect on body condition of the does.

[6] Not determined: 27% of crude fibre.

As for the effect these diets may have on litter performance and body condition of the doe, results are limited, but it is probably related to the maturity level of the females at first mating. Xiccato *et al.* (1999) observed that application of rearing diets enables rabbit does to reach their first effective mating with a lower BW, and to use greater intake during lactation not for improving litter development, but for recovering the actual body condition gap. However, when the does are not inseminated until they reach a suitable BW, the date of the first mating is delayed and the increase in the doe's intake during lactation seems to be destined to increasing their milk production (Pascual *et al.*, 2002a; Martínez-Paredes, 2008).

Recently, Martínez-Paredes *et al.* (2012), comparing different rearing systems, observed that there was no consequence on fertility at first AI when using a low-energy diet during the rearing period, although females reached first mating with lower energy body reserves and lower blood leptin levels than those fed a conventional diet for reproductive does. 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 the fertility rate is affected by many factors, Arias-Álvarez *et al.* (2009) recently proposed that reaching the permissive leptin threshold is 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.

On the other hand, excessive fatness of rabbit females during the rearing period has also been related with high levels of plasma NEFA and glucose and a 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 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 2 yr 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. These authors only observed a trend increasing by 10% the number of kits weaned per year. Martínez-Paredes (2008) reported that the rearing feeding programme used did not affect the main overall productivity traits controlled in 120 reproductive rabbit does over 2 yr (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 to those given the commercial diet *ad libitum* during rearing. Savietto *et al.* (2012a), in a field experiment with 619 females controlled until a minimum of 647 d (only 7% of censored records), observed that young females reared with a fibrous diet lived on average 46.4 d longer than those receiving diet for reproductive does, mainly due to the higher early survival (+4.4 and +5.1% at 1st and 4th parturitions), which led to a significantly higher total production of kits per female reared (+7.4 kits born alive per female).
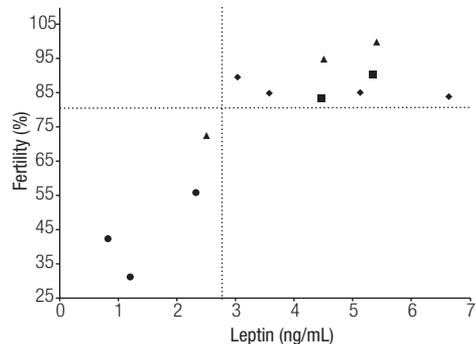

Figure 4: Relationship between leptin levels in the blood of young rabbit does at first mating (16-18 wk of age) and the fertility observed during the 1st reproductive cycle (Martínez-Paredes *et al.*, 2012): ◆ Martínez-Paredes *et al.*, (2012), ■ Arias-Álvarez *et al.*, (2009), ▲ Nicodemus *et al.*, (2007), ● Brecchia *et al.*, (2006).

BODY CONDITION AND REPRODUCTION

As mentioned above, there is a lot of evidence for a genetic component controlling size and mobilisation of body fatness, with high priority in safeguarding body reserves of the animals (Theilgaard, 2006). Not all mobilisations are evoked 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 strongly 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 changes daily during the reproductive cycle and throughout their reproductive life according to their genetically determined level. The problems appear when the animals are forced to deviate from this adequate level, increasing susceptibility to disease, other stress factors and eventual failure (Friggens, 2003).

The body condition of young rabbit females rises until the end of first pregnancy (Figure 3), reaching the peak 10 d before kindling. From this moment to kindling, reproductive rabbit does suffer the highest body reserves mobilisation, with the body condition at parturition showing the lowest level (Savietto, 2013). 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 analysis (BIA; Pereda, 2010). In fact, Pereda (2010) described how the blood concentration of non-esterified fatty acids (NEFA) of primiparous rabbit does reached a higher level at partum (on av. 0.9 mmol/L) compared to that shown at 17 wk of age (0.22 mmol/L) and even at 21 d of lactation (0.33 mmol/L). This is mainly because rabbit foetuses show most of their growth in late pregnancy (almost doubled in the last 3 d; 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 reaching the maximum 10 days after partum (Bolet and Fortun-Lamothe, 2002; Quevedo *et al.*, 2006b; Theilgaard *et al.*, 2006, 2009; Pereda, 2010; Savietto, 2013). Thus, rabbit females would prioritise the current offspring until kindling (devoting a great pre-partum effort), but would prioritise the next offspring immediately afterwards (by promoting a quick recover of reserves 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 can be expected.

However, the evolutionary success of rabbits seems to be more related to the "number" (litter size and reproduction frequency), being one of the 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 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.

Therefore, it could be hypothesised that an adequate amount of body reserves around kindling is important for supporting reproduction in rabbit females. Quevedo *et al.* (2006b) proposed that body condition of rabbit does at partum could condition the AI success at 10 d 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 (2013) depicted the PFT evolution of rabbit females that were effectively and non-effectively inseminated at 11 d of lactation. 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 question this assertion. Several trials, performing comparative slaughters among parturitions, (Xiccato *et al.*, 1992, 2004, 2005; Parigi-Bini *et al.*, 1996) describe frequent negative balances of lactating pregnant rabbit does during their first reproductive cycles. However, in our opinion, the low recovery time after weaning and the large mobilisation occurring at late pregnancy could be more responsible for this negative balance than lactation effort.

In fact, negative balances have sometimes been detected during first lactation; especially in non-pregnant rabbit does which promote milk yield more than body recovery in late lactation (Parigi-Bini *et al.*, 1996; Xiccato *et al.*, 1999; 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, fat mobilisation during lactation was sometimes 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 2 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. As a possible explanation for the different energy balance behaviour observed in lactating rabbit does, Friggens (2003) proposed that animals could be re-adjusting the size of their body reserves to optimise the cost-benefit of having this safety factor (an excess of reserves is costly and a deficit of reserves is dangerous).

Therefore, the main risk of imbalance for reproductive rabbit does arises from those programmes that do not allow recovery of the adequate soma of the female 10 d 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 5).

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 reduces the weaning to next parturition period and consequently the time needed to prepare the female for the pre-partum mobilisation. However, lactation-pregnancy concurrence has frequently been associated with the recovery of body reserves during late lactation, as pregnant rabbit does increase their priority to store reserves for the next litter, the main consequence being 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 on 366162 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
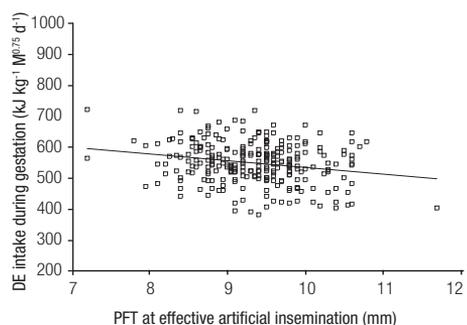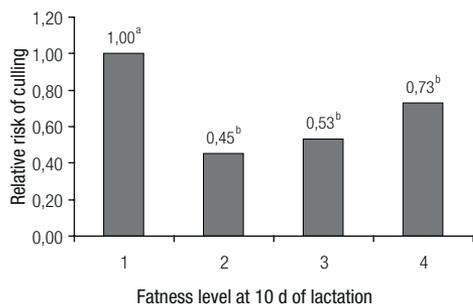

Figure 5: Relationship between the body condition of does at insemination and the energy intake during gestation of rabbit does not showing concurrence with the previous lactation (Quevedo *et al.*, 2006a). DE: digestible energy; $M^{0.75}$: metabolic weight. PFT: perirenal fat thickness. r=−0.22; *P*<0.001.

Figure 6: Relative risk estimates of being culled for reproductive does over 6 reproductive cycles according to fatness level (adapted from Theilgaard *et al.*, 2006). [ab]Bars not sharing superscript are different at *P*<0.05.

resources to be mobilised, but animals carrying excess 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 6). 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 deviations from this optimum level could have negative consequences in reproduction.

GENETIC SELECTION AND RESOURCE 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, including lower fertility, higher rates of metabolic diseases and lower offspring viability (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 and replacement rates of breeding females as high as 110% (Rosell and de la Fuente, 2009). One major handicap 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 constitutes 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), genetic selection programmes of paternal lines in rabbits have traditionally focused on 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), questioning indirect selection (Piles *et al.*, 2004).

In any case, it 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 conversion ratio than those from lines selected for litter size (Orengo *et al.*, 2009). In consequence, animals from these paternal lines selected for growth rate tend 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, 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); in dairy cattle, 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 longevity in both Large White and

Landrace sows (–0.06 and –0.32, respectively), while 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 optimal for fertility and that either lower or higher fat levels reduce fertility by around 10-12% (Castellini *et al.*, 2006). Selection of paternal lines is done according to daily weight gain in the fattening phase, and some of these lines currently present deterioration in their reproductive features, which are clearly inferior to maternal lines (Khalil and Baselga, 2002). However, estimates given in the literature of genetic correlations within breeds (Camacho and Baselga, 1990; Gómez *et al.*, 1998; Garreau *et al.*, 2000; García and Baselga, 2002a; Piles and Tusell, 2012) among litter size or fertility and growth traits are low or zero.

The majority 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 reduction in androgen blood concentrations and high levels of oestrogens (Hammoud *et al.*, 2008). In addition, obesity affects the GnRH-LH-FSH pulses and in turn, by altering Leydig and Sertoli cell functions, modifies sperm maturation (Bélanger *et al.*, 2002). These changes in hormonal 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 research into the possible effect of selection for growth rate on allocation of resources and the possible effect on reproduction and lifespan, as well as on the genetic relationships between growth rate and reproduction (Garreau *et al.*, 2004).

Selection for litter size

From the above proposed inferences relating body condition and reproduction, 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 metabolic resources. On the contrary, negative consequences on body condition and survival should be expected.

Using freezing and embryo transfer techniques (García-Ximénez *et al.*, 1996), Quevedo *et al.* (2005 and 2006b) studied the effect of selection for litter size at weaning on the performance, physiological and productive characteristics of 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 more selected 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 select 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})		
0-21 d lactation	113[a]	117[b]
21-28 d lactation	112	112
Milk production (g/d)		
0-7 d lactation	156[a]	165[b]
8-28 d lactation	215	218

[a,b] Measures without letters in common are significantly different at *P*<0.05.

Mammals have evolved a breeding strategy whereby they fuel their reproductive function 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 in late pregnancy or nursing in the form of milk for the litter in early lactation. Selection experiments show evidence of a relationship between reproduction and body reserves, as selection for prolificacy increases the demand of energy for 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) proposed 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, although they do not show greater energy ingestion or greater mobilisation of reserves. In addition, Quevedo *et al.* (2006b) observed that animals more selected for litter size presented a greater PFT at 10th d of lactation ($+0.12\pm0.06$ mm; $P<0.05$), when females have regained the fitness lost around kindling. Thus, it could be that the selection of animals by reproductive criteria has produced a response correlated with their capacity to obtain resources (van Noordwijk and de Jong, 1986; Reznick *et al.*, 2002).

Similar results have recently been obtained by Savietto (2013), where more selected rabbit females (over 20 generations of selection for litter size at weaning), under conditions of unlimited resources, presented a significantly higher daily feed intake and milk yield in the first week of lactation and a lower milk yield in the last week of lactation. Friggens (2003) proposed that maternal investments for the current litter reach the maximum around parturition in order to contribute to the viability of the newborn litter (Figure 7). Selection for litter size at weaning could have affected the relative priority for the current litter, flattening the shape around kindling to ensure adequate development of larger, but probably less mature litters. Increasing priority for the current litter at the end of pregnancy leads to an extra effort to ensure adequate foetal development, which could be related with the higher reduction in the lactation effort observed at the end of lactation of the previous reproductive cycle and the high mobilisation observed at the end of pregnancy (Savietto, 2013). 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 in 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 dependent on maternal milk– will not improve the litter's chances of survival.
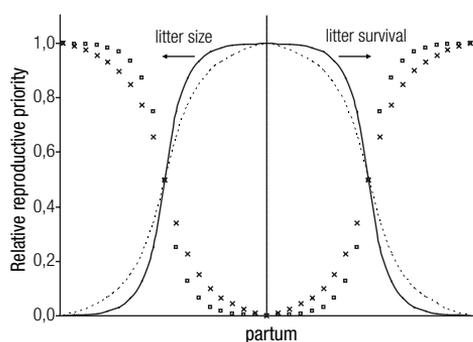
Figure 7: Proposal for evolution of the relative reproductive priority for the current [less (······) and more (——) selected for litter size] and future litter [less (× × ×) and more (▫ ▫ ▫) selected for litter size] in rabbit females from conception to weaning. The priority accorded the current litter is assumed to be the maternal investment rate scaled from 0 to 1, as proposed by Friggens (2003).

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

However, under a nutritionally restricted environment, Savietto (2013) 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 contrast, the main female body traits controlled were less affected by the feeding restriction in more selected animals. These results suggest that selection for litter size could increase the susceptibility of animals to this type of environmental challenge, which leads to a change in nutrient partitioning to reduce the performance under feeding restriction.

But why does selection for litter size lead to more environmentally sensitive animals? As proposed above, the fitness characteristics enhanced under this selection criterion are "the number". When the

resources available are limited, the success of the current litter could be questioned; thus, the animal probably decides to reduce the priority for the current litter (addressing a relatively lower amount of resources to those traits directly related to the current litter performance, such as energy intake and milk yield), while the next litter seems to be prioritised by increasing the body reserves (the fuel for the future litter). Therefore, when animals are selected for reproductive traits such as litter size and the resources available are limited to the present, they are unable to ensure the success of the current litter. When this happens, maternal investment for the current litter is reduced (and in consequence the animals seem less robust –or more sensitive to the environment–) to concentrate their efforts on ensuring the next one (Friggens, 2003), when perhaps resources and environment could be improved.

Selection for longevity

Longevity reflects the animal's ability not to be culled or die. The main reasons for culling in animal production include diseases, low fertility and low production (Vollema, 1998). In 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 improved dietary formulation and management. Focusing 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 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 were 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 over seven generations with a control line, no difference in longevity was found (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 [consisting of hyper selection of animals with 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 3 cycles. However, when animals were subjected to a non-programmed restricted environment (change of nutritional management to feed restriction after weaning) in one of the farms from the 3rd reproductive cycle, litter size at birth of V line females was depleted as of this moment, while those from the LP line maintained their prolificacy at the expense of a reduction in their greater soma (Figure 8). Theilgaard
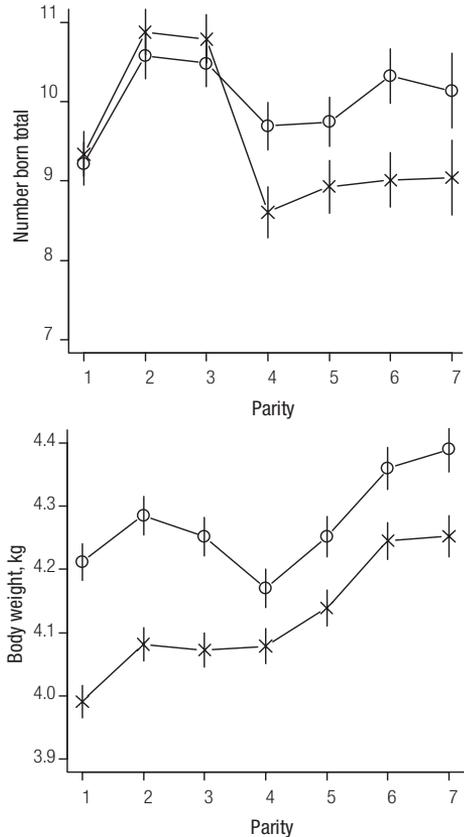

Figure 8: Effect of genetic line (LP: –O– and V: –×–) on the evolution of the total number born and female body weight at partum (adapted from Theilgaard *et al.*, 2007).

et al. (2007) hypothesised 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.

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 kits) during their 2nd lactation. Longevous productive 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 lower fat mobilisation (–0.11±0.03 mmol of NEFA; $P<0.05$) at the beginning of lactation, confirming the advantage of the greater soma of this type of animals in confronting productive and environmental challenges. In fact, LP does showed a greater milk yield than V does, even per kg of metabolic weight (+5±2 g kg^{-1} BW$^{0.75}$ day^{-1}; $P<0.05$), and especially when lactation pressure increased (9 kits).

This greater soma of rabbit females selected for reproductive longevity seems to allow them to better cope with the possible productive challenges that they may 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. So, 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 the availability of resources is not limited, more selected animals can successfully cope with most of their higher needs without too many negative consequences. In fact, it is not uncommon 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 is when animals suffer discrete but not infrequent and even cyclical suboptimal environments (i.e. resources limitation, heat stress, immunological challenge) that the greater susceptibility of high producing animals to these stressing conditions appears (Schinkel *et al.*, 1999; De Greef *et al.*, 2001; Yalçin *et al.*, 2001; Windig *et al.*, 2005).

Knap (2005) defined the concept of robustness in a 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 hypothesised 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 helped increase their robustness.

With this aim, Savietto (2013) and Savietto *et al.* (2012b) 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 2 reproductive cycles.

The results of this work show how, when resources were limited, LP females compensated 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 than that observed under non-limiting conditions. So, LP females were able to maintain their milk yield, litter growth and body condition unaffected, as well as the litter size at the 2nd kindling, while V females reduced their milk yield trying to maintain their body condition and next litter size. During the 2nd lactation, LP females had a lower milk yield than that observed under non-limiting conditions, but without any negative effect on their body condition or on the litter performance at 3rd birth. In contrast, V females in restricted conditions presented a continuous worsening of their main performance traits (milk yield and body condition), with the size of their litters at the 3rd kindling clearly being affected (−1.8 and −2.6 total and alive kits born, respectively; $P<0.05$).

For a better picture of environmental sensitivity, the response graphs in Figure 9 represent the effect of genotype (V or LP) on dietary energy intake, body reserves and kits born alive depending on the dietary energy (normal or restricted). For all traits examined, the response to environment restriction of females coming from a line founded for reproductive longevity criteria was flatter than that obtained from females selected for litter size at weaning, highlighting their differences in robustness. Under non-limiting conditions, females selected for reproduction show their superiority in prolificacy, but when environment quality worsens these animals show greater reduction in their ability to obtain resources and maintain body reserves and reproductive performance.

In other species, signs of reduced robustness have also been observed 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 optimised towards the best adaptation of the individual to its environment (fitness). Therefore, when we genetically select for reproduction traits, resources could logically be redirected towards these reproduction traits at the expense of other traits (such as robustness traits), which lead to genotype×environment interaction. However, the resource allocation theory also considers the possible development of nutrient partitioning strategies that allow the animals to obtain additional
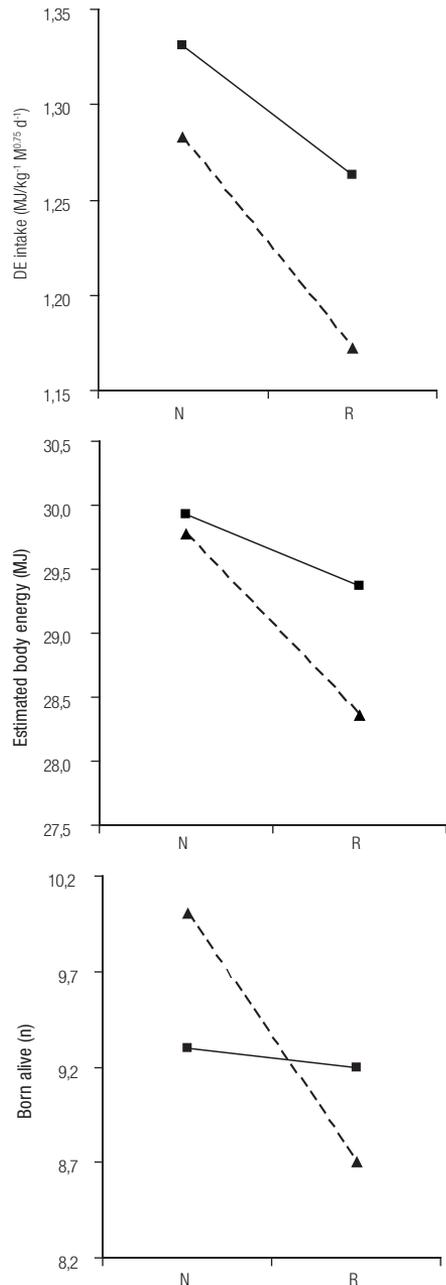

Figure 9: Reaction norm for the effect of genetic type (■ LP and ▲ V) on average estimated body energy, digestible energy (DE) intake and number of kits born alive (2nd and 3rd kindling) according to dietary environment [normal (N) *vs.* restricted (R)]. $M^{0.75}$: metabolic weight.

resources for optimised reproduction without penalising robustness, or to optimise resource allocation through time to ensure their fitness success.

These results highlight the improvement in robustness characteristics when rabbits are selected or founded for reproductive longevity criteria. These criteria would provide the animals with additional tools for more appropriate 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 sensitive to the nutritional challenge, robust females are able to maintain most of their reproduction traits unaffected, which could help confer their reproductive longevous character.

Another component in the definition of the female's lifespan is her susceptibility to the common diseases that could appear on the rabbit farms. Possible changes in resource allocation as a consequence of genetic selection or reproductive management should lead the female to situations where body condition could be withdrawn from the adequate level, increasing the susceptibility of animals to occasional immunological challenges. For example, the greatest drop in body reserves takes place at the end of gestation, which is the time of greater elimination of commercial does on the farm (Rosell and de la Fuente, 2009) and the lowest B lymphocyte counts in blood (Ferrian *et al.*, 2012), and an excessive mobilization of the reserves at parturition conditions the success of mating during the following lactation (Quevedo, 2005; Savietto, 2013). These results would reflect the importance of not moving too far from the appropriate body status to ensure reproduction and reduce the risk of culling. Thus, Guerrero *et al.* (2010) and Ferrian *et al.* (2012) observed 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). Moreover, 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 susceptibility 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) recently reported how selection for litter size over 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 these populations in the blood of more selected females from the 1st to the 2nd parturition. In addition, this work also reported an increase in the lymphocyte counts (total and T CD5+) of "more robust" females under heat compared to normal conditions when lymphocyte populations showed the lowest value (2nd parturition), while "less robust" females counts remained invariable. Other recent works (Savietto *et al.*, 2011; Ferrian, 2013) would show indications in favour of the theory about a possible improvement of the immune system modulation in robust animals (lower susceptibility to challenge with LPS, or lower mortality of their kits during the fattening period), although further research efforts should be made in the future to confirm this matter.

CONCLUSIONS

The present review provides enough evidence about how nutrient partitioning between the different metabolic functions throughout rabbit female life is genetically driven. Consequently, allocation of resources in the female rabbit takes place to ensure their genetic selection success at all times. Therefore, if rabbit females have been selected by a reproduction criterion, such as viable litters produced in a lifetime, nutrient partitioning is defined as the optimal trade-off between the maternal investments addressed to current and future litters to maximise the number of viable litters produced in a lifetime. On the other hand, the constitution of a line through high selection intensity in its foundation by reproductive longevity has led to rabbit females characterised by a higher robustness. Particular nutrient partitioning enables the robust females to better cope with possible reproductive, environmental, and immunological challenges that they may meet in the course of their productive life, thus explaining their greater life expectancy on the farm.

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