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THE NUTRITIONAL STATUS OF FOETUSES AND SUCKLING RABBITS AND ITS EFFECTS ON THEIR SUBSEQUENT PRODUCTIVITY: A REVIEW

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INTRODUCTION

In multiparous animal species a number of production traits are influenced by maternal effects prevailing during gestation and the suckling period. Nutrient supply to embryos and foetuses is exclusively dependent upon the mother, but subsequently the level of the milk production of the doe plays a determinant role between birth and weaning. Maternal effects influencing the individual foetuses and the whole litter during gestation are exhibited in body weight at birth, while the degree to which the individual suckling rabbits are supplied with the doe's milk is determined primarily by litter size. It is generally not possible to distinguish between the maternal effect exerted during gestation and that present during the suckling period, as offspring born in larger litters have lower birth weight than average. In their attempts to suckle these young rabbits face greater competition from a larger number of littermates.

The major factors affecting birth weight

Breed

The genotypes of both the mother and the foetuses play a decisive role in determining birth weight. When breeds of different body size are crossbred, or their embryos are transferred to does of another breed, the size of the mother exerts a substantial effect on the weight at birth of the offspring. A study similar to the classic experiment performed with Shire horses and Shetland ponies by WALTON and HAMMAND (1938) was carried out with rabbits by VENGE (1953). The main findings of this experiment are summarised in Table 1.

Table 1. Growth in large- and small-bodied breeds if born to and reared by their own mother, if transplanted into the other breed as foetuses, and if exchanged when newborn (Venge, 1953).

Age (days)	Large breed			Small breed		
	normal birth & rearing	transplanted into smaller breed	exchanged when newborn	normal birth & rearing	transplanted into larger breed	exchanged when newborn
0	70	51	60	41	65	55
7	180	113	145	97	173	110
14	306	160	248	164	287	160
21	390	244	396	220	398	206
28	613	372	561	299	495	329
42	1152	721	1100	517	793	585
56	1573	1232	1402	694	949	709

Birth weight in the large breed decreased by 27 %, while that in the small breed increased by 59 %, when the foetuses were transplanted into does of the other breed. The body weight of the doe plays an important role in this effect. The size of her uterus and the degree of nutrient supply to the foetuses (by the effect of blood supply) are predominant factors. A generally valid correlation is that as the body size of the doe decreases, the weight at birth of her young is also reduced (HOLDAS and SZENDRŐ, 2000). In giant breeds the characteristic weight at birth is 63 to 66 g. In medium-sized, commercial meat rabbit breeds and hybrids average birth weight is 60 to 65 g but only 55 to 58 g in coloured (medium-sized) breeds and 45 to 50 g in small breeds.

Litter size

Decrease in litter size is accompanied by an increase in average individual birth weight (DUNCAN, 1969; VAN DEN BROECK and LAMPO, 1975; LEBAS, 1982; SZENDRŐ, 1986; DIM *et al.*, 1990; GARCIA-XIMENEZ and VICENTE, 1993; BOLET, 1994; BOLET *et al.*, 1996; SEITZ *et al.*, 1998), as the degree of nutrient supply per foetus during the gestation period is more favourable in does carrying fewer young. Phenotypic correlations of r = -0.33 to -0.46 between litter size and individual birth weight have been established (KROGMEIER and DZAPO, 1991; LAMPO and VAN DEN BROECK, 1975; MOURA *et al.*, 1991; POLASTRE *et al.*, 1992; SZENDRŐ, 1993). It was ascertained by SZENDRŐ (1978) that in litters of 6 to 11, where the size of the litter increased by one, mean body weight at birth decreased by 1.9 g. The relation between litter size and birth weight is not a linear one. There are more substantial weight differences between the young in smaller litters than in larger ones.

Kindling number

The number of litters previously produced by the doe, if any, also influences the growth of the foetuses in the uterus. The birth weight of the progeny of nulliparous does is substantially lower than that of the offspring of multiparous does (MATHERON, 1982, LUKEFAHR *et al.*, 1983c; AFIFI *et al.*, 1988; BASELGA *et al.*, 1992; VICENTE and GARCIA-XIMÉNEZ, 1992; FARGHALY, 1996; NOFAL *et al.*, 1996; BOLET *et al.*, 1996; ARGENTE *et al.*, 1996a; HAMILTON *et al.*, 1997; EIBEN *et al.*, 1998, SZENDRŐ *et al.*, 1999). Studies by PARIGI-BINI and XICCATO (1993) and VASQUEZ *et al.* (1997) found birth weight to be 6 to 10 % lower in nulliparous than in multiparous does. As does are first mated or inseminated when they reach 75 to 80 % of their adult body weight, during their first pregnancy a considerable proportion of the nutrients available is still being used for the development of their own tissues, to the detriment of the foetuses.

VÁSQUEZ MARTINEZ *et al.* (1999) reared the progeny of nulliparous and multiparous does, which were of lower and higher weight respectively, using their own mother or one from the other group. Thus, suckling rabbits of lower or higher birth weight, born to younger or older does respectively, were reared either by a nulliparous doe whose milk production was still at a reduced level or by a multiparous one which produced higher quantities of milk. The effect (both pre- and postnatal) of the original mother (expressed in terms of birth weight) and the foster mother (through her milk production) could be detected up to the age of 12 weeks. The most pronounced differentiation was observed between kits born to younger does and those produced by older ones. The birth weight of the young, influenced by the age of the mother, still significantly affects body weight at 3 weeks, but this effect diminishes in the course of their development.

In his review, XICCATO (1996) provided a comprehensive overview of the energy deficit arising in does during their first pregnancy and suckling, which leads to lower body weight in the first litter. In the final third of the gestation period there is a reduction in protein and fat within the body of the doe, and also a decline in the transfer of energy to the foetuses. Since the doe also has to devote energy to her own weight gain, she does so partly to the detriment of the foetuses.

Physiological status

When suckling does were compared with non-suckling controls, both groups being inseminated immediately subsequent to parturition, FORTUN *et al.* (1993) observed a 20 % difference in the weight of the foetuses, despite the fact that feed intake in the suckling does was 78 % higher. In another study non-suckling does and does rearing litters of either 4 or 10 young were compared (FORTUN and LEBAS, 1994). Foetal weights recorded in these three groups were 39.7, 37.5 and 34.9 g, respectively. The above findings provide evidence that when does are concurrently suckling and pregnant, the production of milk has a negative effect on the growth of the foetuses, and this effect becomes stronger with increase in the quantities of milk produced by the doe (i.e., with increase in the size of the litter she is suckling). Does are not capable of increasing their feed intake to such a degree as to ensure that a sufficient supply of nutrients is available to the foetuses they are carrying. LUBLIN and WOLFENSON (1996) obtained evidence that poorer blood supply to the uterus is responsible for this: in their study the uterine blood flow to the maternal placenta decreased by 18 % during lactation but increased by 50 % in non-pregnant does. This is evident, as there is also substantial blood supply to the mammary glands in lactating does.

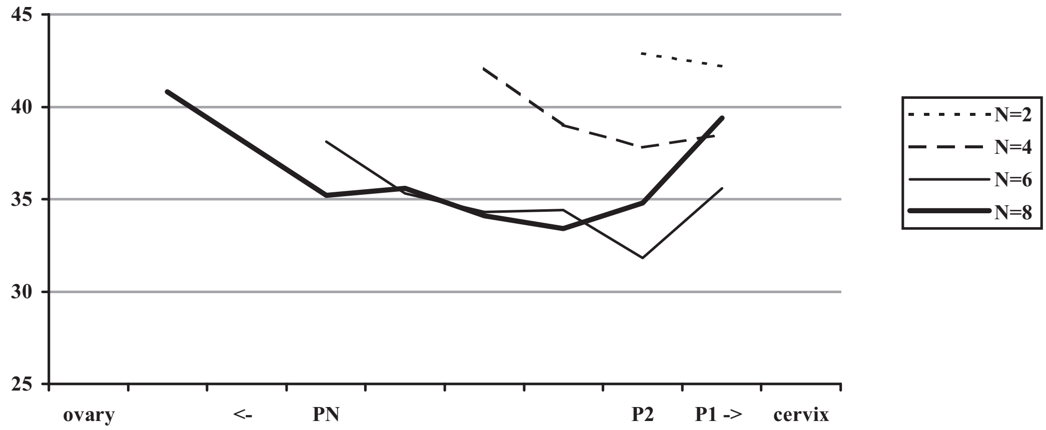
Nutrition

FORTUN *et al.* (1994) and FORTUN-LAMOTHE (1998) observed a significant decrease in the weight of foetuses carried by does which were subjected to different degrees of feed restriction maintained for various periods during gestation. Based on the processing of a quantity of data from the literature, ROMMERS *et al.* (1999) ascertained that in most instances the energy level of the diet fed to the doe influences birth weight (higher energy level, greater weight), but no effect is exerted by dietary energy source. MAERTENS and DE GROOTE (1991) found that the doe needs to build up an energy reserve in her body in the first half of the gestation period, as there occurs a transfer of energy from the body of the doe to the foetuses in the final week of pregnancy.

Intrauterine position of foetuses

DUNCAN (1969), LEBAS (1982) and SANTACREU *et al.* (1994) examined the weight of foetuses at 25 to 28 days in relation to their position within the uterine horn. When between 2 and 7 foetuses were present within an uterine horn, the position nearest to the oviduct was found to be the most favourable. The weight of the foetuses decreased with increasing proximity to the cervix. In addition LEBAS (1982) also observed that, despite the above tendency, when between 4 and 6 foetuses were present the foetus with the lowest weight was to be found not directly adjacent to the cervix but in the second position away from it. Studies by PÁLOS *et al.* (1996) revealed that when several foetuses were developing in the uterine horn the smallest was situated in the second or third position from the cervix in intact does (*Figure 1*), while (POIGNER *et al.*, 1998) established that the smallest foetus was always the second from the cervix in unilaterally ovariectomised does.

Fig. 1: The effect of number and position of rabbit embryos in the uterine horn on their weight at 30 days of pregnancy *(The position of foetuses in the uterine horn was numbered from the cervical end (P1, P2…) to the end nearest to the oviduct; PN, where N is the number of foetuses in the uterus)*
(Pálos et al., 1996)



LEBAS (1982) found that the growth of the offspring developing in any uterine horn examined is independent of the number of foetuses present in the neighbouring uterine horn. This is borne out by the findings of studies performed by HAFEZ (1964). However, PÁLOS *et al.* (1996) ascertained that if the other uterine horn contained more than the average number of foetuses the weight of those in the horn examined was reduced, irrespective of position.

There may be two main reasons behind the relation between the position of foetuses within the uterus and their weight. One of these reasons is the size of the space available to them, the other being the difference in efficiency of the blood supply to the foetuses in the individual positions. A certain amount of space is also necessary for successful implantation to be achieved. Studies performed by HAFEZ (1964) indicated that implants needed to be 2 mm apart or more to be well-spaced. Narrower spaces resulted in neighbouring implants becoming crowded or fused.

The blood supply to the different parts of the uterus also varies (DUNCAN, 1969; HAREL *et al.*, 1978). Each uterine horn is supplied with blood from its cranial end by the ovarian artery reaching it from the direction of the ovary, the caudal branch of which forms an anastomosis with the lateral branch of the uterine artery. Hence, the end of the uterine horn nearer to the oviduct in fact benefits from a dual blood supply (DUNCAN, 1969; DEL CAMPO and GINTHER, 1972; WALDHALM and DICKSON, 1976), which results in a more favourable supply of nutrients to the foetuses developing here.

TSUTSUMI and HAFEZ (1964) established that the number of maternal arterial vessels penetrating into the maternal placenta varies between 4 and 12, and the number of maternal venous vessels between 1 and 6. SANTACREU *et al.* (1994) determined the level of blood supply to individual foetuses on the basis of the number of veins in their vicinity. They ascertained that foetuses at the bottom of the uterus were better irrigated, irrigation being less efficient in those situated slightly higher.

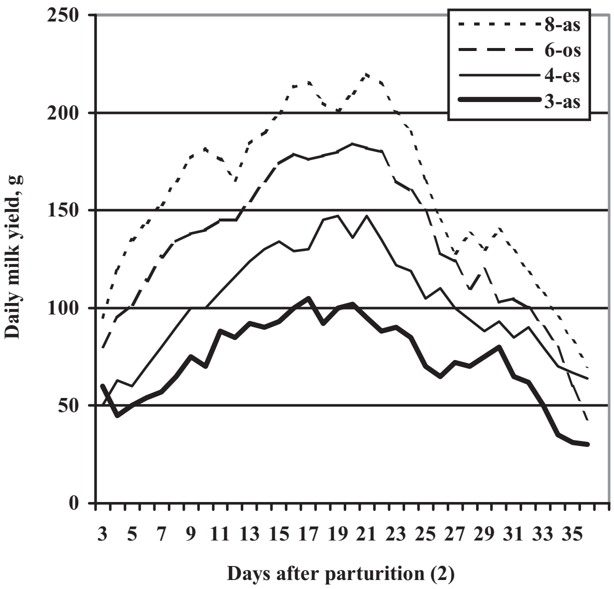
DUNCAN (1969) demonstrated a very clear correlation between placental weight, foetal weight and placental blood flow. Foetal weight was the highest and placental blood flow the strongest at the ovarian end of the uterus, both decreasing towards the vagina. Depending on the size of the litter under examination, in a number of instances the values recorded for the position nearest to the cervix was found to be slightly higher.

The effect of birth weight on other production traits

Mortality

Within any given rabbit breed there is a close correlation between the weight of offspring at birth and their viability. Studies performed by SZENDRŐ (1978) and VICENTE and GARCIA-XIMÉNEZ (1992) revealed that, with reference to medium-sized breeds (New Zealand White and Californian), rabbits born weighing less than 35 g were non-viable when the litters were not homogenised for weight. However, even among those weighing between 35 and 40 g at birth, only half reached the age of one week. Birth weight below which the chance of survival is at a critical level can be estimated at around 40 to 45 g. In an experiment with New Zealand White rabbits SZENDRŐ and BARNA (1984) ascertained that acceptable viability (i.e., mortality below 10 %) can be anticipated from newborn rabbits weighing more than 55g (*Figure 2*). SEITZ *et al.* (1998) recorded 77 % mortality among rabbits weighing less than 30 g and 10 % among those weighing more than 70 g.

Fig. 2: Milk production (lactation curve) of rabbit does in relation to litter size
(Torres et al., 1979)



The higher mortality characteristic of rabbits of low birth weight can be attributed partly to their reduced viability and partly to their low milk intake. This results from the disadvantageous position in which they find themselves in the struggle against their larger littermates for milk during the few minutes spent suckling each day (SZENDRŐ, 1993; HUDSON *et al.*, 1996; XU, 1996). GARCIA-XIMENEZ and VICENTE (1991) estimated the number of viable offspring which could potentially be produced per female. In the four lines they examined the minimum birth weight consistent with survival was between 40 and 45 g.

It frequently occurs that young rabbits fail to suckle sufficient amounts of milk on odd occasions, but this is not of critical significance from the aspect of their survival unless they also fail to suckle enough on the subsequent day (LEBAS, 1975; HUDSON *et al.*, 1996).

Weight gain

Low birth weight is unfavourable with respect to weight gain during the suckling period. This can be explained partly by lower weight in itself, and partly by the disadvantageous situation of smaller suckling rabbits in relation to their larger littermates. Studies by SCHULTE and HOY (1997) indicated that birth weight was correlated with milk intake ($r = 0.43$), daily weight gain ($r = 0.52$) and weight at weaning ($r = 0.40$). Neither did they find evidence of compensation subsequent to weaning. Thus, even up to the time of slaughter, rabbits were not capable to compensate for any weight lag which may have developed before they switched to solid feed.

Factors influencing litter size

Heritability and selection

The heritability of litter size is characteristically weak, with an h^2 value of around 0.1 to 0.2 (KHALIL *et al.*, 1986; BASELGA *et al.*, 1992; FERRAZ *et al.*, 1992; KROGMEIER *et al.*, 1994; GOMEZ *et al.*, 1996; CIFRE *et al.*, 1996; FERRAZ and ELER, 1996; ROCHAMBEAU, 1997; PÉREZ-ENCISO and BIDANEL, 1997). This low h^2 value indicates that the various environmental factors play an important role in determining litter size.

Different research groups have occasionally given diverse assessments of the possibility for selection for increased litter size. ROCHAMBEAU *et al.* (1994) and GOMEZ *et al.* (1996) expressed the view that rabbit selection oriented towards litter size at birth or at weaning leads to slow but steady genetic progress. On the other hand, a number of researchers are of the opinion that selection for litter size holds out only a meagre hope (RINALDO and BOLET, 1988; BASELGA *et al.*, 1992; BLASCO *et al.*, 1994; ARGENTE *et al.*, 1996b). These researchers consider indirect selection to be more expedient. They recommend simultaneous genetic selection for the traits which are components of litter size, but which, taken individually, are more strongly heritable traits than litter size itself (ovulation rate, prenatal mortality and uterine capacity).

The true position probably lies between these two viewpoints, in that, alongside litter size, in practice it is advisable also to take into account at least one component trait.

Kindling number

The size of the litter produced by a doe at her first kindling is substantially lower than the average number born in subsequent litters (MATHERON, 1982; LUKEFAHR *et al.*, 1983c; SZENDRŐ and VARGA, 1986; AFIFI *et al.*, 1988; BASELGA *et al.*, 1992; VICENTE and

GARCIA-XIMÉNEZ, 1992; FARGHALY, 1996; NOFAL *et al.*, 1996; BOLET *et al.*, 1996; ARGENTE *et al.*, 1996a; HAMILTON *et al.*, 1997; EIBEN *et al.*, 1998). The largest litter size at birth is to be anticipated at the second or third kindling (VAN DEN BROECK and LAMPO, 1975; SZENDRŐ; 1986; BASELGA *et al.*, 1992), after which a gradual decrease is observed.

Studies by MATHERON (1982) found the mean number of ova released in nulliparous Californian and New Zealand White does to be 2.44 lower than in older does. Alongside higher ovulation rate, higher embryonic and foetal mortality rates are also characteristic of multiparous does (MATHERON, 1982; BASELGA *et al.*, 1992).

Frequency of kindling

When does are inseminated *post partum* the rate of prenatal mortality also rises in consequence lactation in parallel with pregnancy (FORTUN *et al.*, 1993; FORTUN and LEBAS, 1994). The number of offspring being suckled exerts a negative influence on the growth of the foetuses developing in the uterus (FORTUN and LEBAS, 1994; DEPRES *et al.*, 1996; BLASCO *et al.*, 1992; THEAU-CLÉMENT *et al.*, 1996). As a result, in does producing litters in close succession litter size is lower than the size characteristic of less frequent mating, as are both litter weight and individual weight at birth (SZENDRŐ, 1993; SZENDRŐ *et al.*, 1999).

The effect of litter size on certain production traits

Mortality

ARGENTE *et al.* (1996a), KROGMEIER and DZAPO (1991) and RAO *et al.* (1977) found that the relation between litter size and mortality among suckling rabbits is a very weak one. Neither did KHALIL *et al.* (1986) find evidence of any clear-cut relation between these two parameters. Litter size appeared to exert no influence on the survival of the young. SZENDRŐ (1993) also reported a weak negative correlation, expressing the opinion that the correlation coefficient does not provide a correct portrayal of the relation existing between the two parameters, as increased mortality is observed in both very small and large litters (MAERTENS and LUZI, 1995). In small litters total litter loss is a more significant cause of suckling mortality, while in large litters weak viability arising from low birth weight is responsible for increased mortality (SZENDRŐ, 1986) (*Figure 3*).

Milk production and milk intake

At every point in the lactation period the milk production of rabbit does is higher where litter size is greater (*Figure 4*). Increase in the number of young in the litter inversely affects the quantity of milk available per suckling rabbit. Young rabbits reared in larger litters have access to less milk, which leads to reduced weight gain (SZENDRŐ, 1993). The correlation between litter size and the amount of milk available per suckling rabbit has been determined at r = -0.35 (LEBAS, 1975). FERGUSON *et al.* (1997). ascertained correlations of r = -0.46 in the first week, r = -0.41 in the second week and r = -0.51 in the third week of lactation. The negative effect exerted on weight gain by increased litter size is detectable particularly up to the age of 3 weeks. It is chiefly after the 10^{th} day of lactation that young rabbits reared in larger litters are at a disadvantage.

Fig. 3: Daily weight gain of rabbit kits in relation to litter size (Szendrő, 1986)

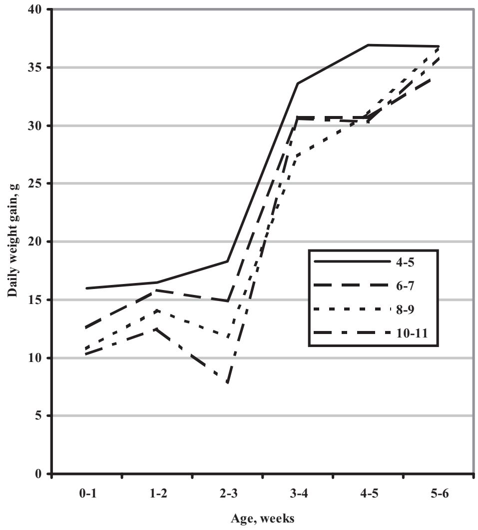
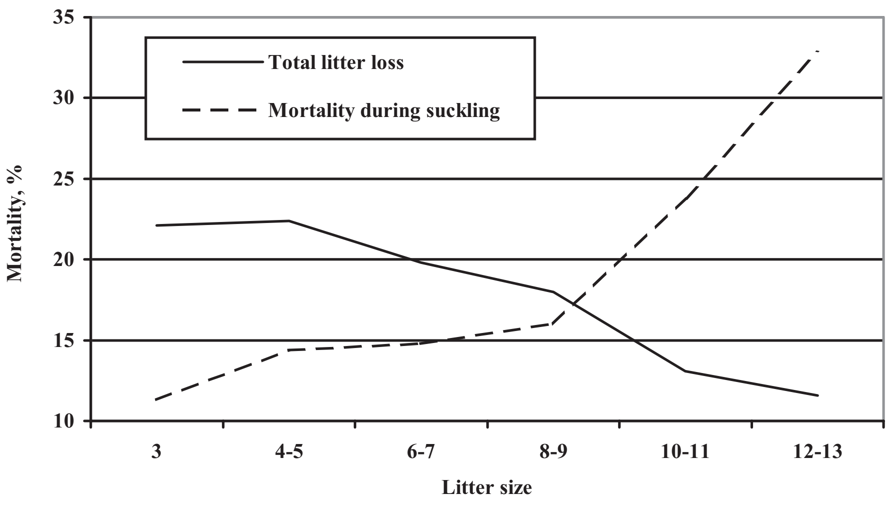


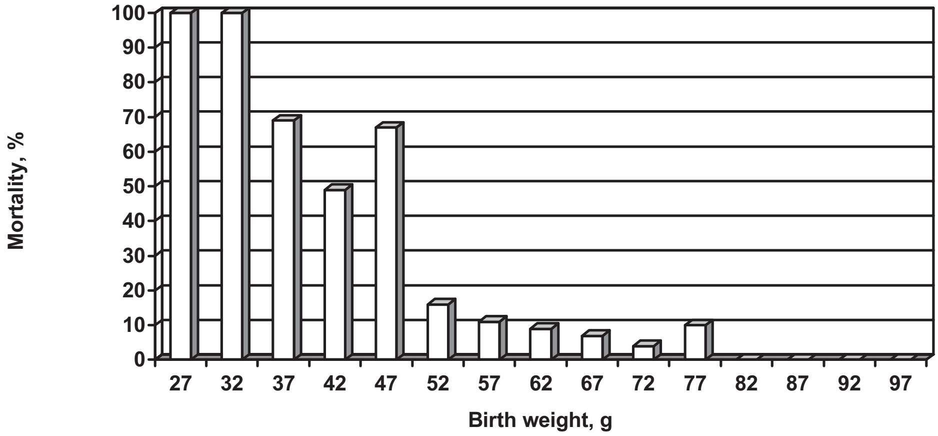
Fig. 4: Effect of litter size at birth on total litter loss and suckling mortality in rabbits (Szendrő and Barna, 1984)



In a study involving high production does MAERTENS and DE GROOTE (1991) observed the highest weight gain among the young on the 9th day of lactation. Subsequently weight gain decreased up to the point at which the young rabbits began to eat significant quantities of solid feed. This indicates clearly that from the 9th day of lactation the milk production of the doe could no longer meet the requirements of the suckling rabbits for maximal growth.

SZENDRŐ (1986) compared individual weight gain in litters of 4 to 5, 6 to 7, 8 to 9 and 10 to 11 (*Figure 5*). From this comparison it was established that in the third week, taking the weight gain of the litters of 4 or 5 as 100 % (18.8 g per day), the other groups achieved weight gain of 79, 63 and 42 % respectively. This indicates that pronounced starvation occurs in this period in rabbits reared in larger litters, their growth being limited by the milk production of the doe. VICENTE and GARCIA-XIMENEZ (1992) also established that both the ability of the doe for milk production and competition between suckling rabbits limits the maximum expression of genetically determined ability for growth.

Fig. 5: Effect of birth weight on mortality in the first week in suckling rabbits (Szendrő, 1986)



Weight gain and body weight

The relations between litter size and birth weight, between litter size and milk production, and between litter size and the quantity of milk available per suckling rabbit influence the development of body weight among the young. Litter size exerts a positive effect on litter weight and a negative influence on individual weight.

A number of researchers have demonstrated, by means of genetic analysis of weight at weaning, the negative effect of litter size on subsequent weight gain (ZIMMERMANN *et al.*, 1988; BRUN, 1993; BRUN *et al.*, 1992; POLASTRE *et al.*, 1992; MCNITT and LUKEFAHR, 1996). This effect has still been detected at the end of the fattening period, at the age of 10 to 12 weeks. On the other hand in terms of weight gain, maternal effect prevailing through litter size can only be detected up to the age of 6 weeks. During the fattening period this maternal effect loses its significance, although neither is there any evidence of compensation (BLASCO *et al.*, 1983; SZENDRŐ, 1984). MCNITT and LUKEFAHR (1996) found that the effect exerted on weaning weight by the constant maternal environment is approximately a third as strong as the effect of litter size. The role of the maternal environment with respect to weight gain during the fattening period is negligible by that time, and the direct genetic effects begin to increase in significance.

BOLET *et al.* (1996) monitored the effect of the number of embryos developing in the uterine horn (i.e., litter size) up to the age of 11 weeks. Their conclusion was that the lower weight of progeny in large litters, which remains low after birth and weaning, was mainly due to competition for nutrients. The effect of litter size on body weight can be detected even after rabbits have reached slaughter weight. On examination of weight gain in rabbits reared in litters of 6, 9 or 12 ROMMERS *et al.* (2000) ascertained that the significant difference between the litters of 6 and 9 which was found to develop during the suckling period ceased 5 weeks after weaning, while the weight lag of the litters of 12 only disappeared during the first lactation period. Hence, in absence of the effect of different birth weight (as birth weight corresponded between the groups) the effect of the level of nutrient supply during the suckling period may remain for a long time after weaning.

Doe performance

BABILE and MATHERON (1980) and BLASCO *et al.* (1992) observed that the weight of does originating from larger litters was lower at first insemination than that of does from small litters.

The correlation between adult body weight and ovulation rate is a positive one (HULOT and MATHERON, 1979; BLASCO *et al.*, 1992). KHALIL *et al.* (1986) expressed the view that ovulation rate among does originating from larger litters was lower than that characteristic of their mothers. Thus, if a doe produces a larger litter, her direct female offspring will give birth to litters which are smaller than the average, and the litters subsequently produced by her granddaughters will again be larger. Thus, with respect to litter size there exists a negative relation between the direct genetic and the maternal effect, and a positive correlation between the direct genetic and the grand-maternal effect (ROUVIER *et al.*, 1973).

BABILE and MATHERON (1980), SZENDRŐ *et al.* (1989), BÍRÓ-NÉMETH and SZENDRŐ (1990), and later TUDELA *et al.* (1998) established that the number of progeny in the litter in which does were born and reared exerts a negative effect on their subsequent reproductive performance: that is, the larger the litter from which the doe originates, the weaker her level of production as an adult. However, SZENDRŐ *et al.* (1989) found that, in contrast with the findings of studies performed on other animal species, in the case of the rabbit there is no strictly regular pattern by which birth into a larger litter would always lead to deterioration in the adult reproductive performance of does. Substantial differences have been encountered between the various genotypes. It has also been observed that does originating from the largest litters are, in most cases, also capable of attaining excellent production results. The above observations are also corroborated by the results of a study performed by BÍRÓ-NÉMETH and SZENDRŐ (1990). In a manner similar to that observed in the case of the findings outlined above, these authors observed that when does are born into litters of between 3 and 8 their subsequent performance declines with increase in size of litter of origin. On the other hand, does originating from litters of nine or more achieve considerably more favourable results than would be anticipated on the basis of the above tendency.

In the experiments referred to above the birth weight of the young was also generally lower in larger litters. Therefore, it is not possible to distinguish precisely which of these two factors was responsible for the effect which prevailed. After rearing young rabbits of identical birth weight in litters of different sizes (6, 9 or 12), ROMMERS *et al.* (2000) demonstrated that not only did does reared in litters of 12 have significantly lower weight when first mated than those reared in litters of 6, but substantial differences in body composition at first mating were also ascertained, the primary one being lower total body fat content in the does originating from the litters of 12. Nulliparous does reared in litters of 12 produced significantly smaller litters than those reared in litters of 9. The results for the first insemination, performed at the age of 14½ weeks, proved particularly weak.

POIGNER *et al.* (1999) examined the effects of birth weight and litter size separately. They established that at first insemination does of low birth weight (39 to 43 g) became pregnant significantly more readily, but at subsequent inseminations the pregnancy rate was similar in all the groups. On the other hand, litter size (total born and number at weaning) proved greater for does of high birth weight (63-70 g) when all kindlings were evaluated together. However, in this instance the effect of litter size was not significant.

Conflicting genetic and maternal effects exert influence on the effectiveness of selection for litter size. This is also verified by an experiment of classic status carried out by FALCONER (1960), who performed divergent selection for large and small litter size. This selection initially yielded results which were contrary to expectations, the number of young per litter being observed to decrease in the line developed from plus variants, but to increase in the minus variant line. The results of this experiment indicated that in the first generation the negative maternal effect prevailing through litter size during the rearing period counteracted the genetic superiority of the does. The situation changed in the course of the subsequent generations, litter size then developing in accordance with expectations.

CONCLUSIONS

Selection

The observations summarised above provide uniform evidence that pre- and postnatal maternal effects exert a substantial influence, primarily through birth weight and litter size, on the production of suckling and growing rabbits. Indeed, under certain circumstances these effects even manifest themselves in the subsequent production performance of does.

In the selection and crossbreeding of the maternal lines of the hybrids which are now gaining increasingly greater ground in the world a prime objective is to increase litter size. As a result of selection through 17 generations performed in INRA lines a substantial increase in litter size has been attained, but also, in parallel with this, a similar rate of reduction in the weaning weight of the rabbits produced has been observed (ROCHAMBEAU DE, 1998). Other authors (KHALIL *et al.*, 1987) have also drawn attention to this phenomenon; they expressed the view that selection for litter size would be accompanied by a decrease in average weaning weight.

The situation is exacerbated by the fact that the energy balance is negative in primiparous suckling does (XICCATO, 1996). Higher dietary energy levels do not lead to improvement in foetal survival or growth in primiparous does concurrently lactating and pregnant. The knowledge presently at our disposal suggests that there is no rabbit diet available which has the capacity to remedy the above concerns.

The long-term objectives set should include genetic improvement programmes of such a nature as to take into account not only litter size, but also litter weight (and individual birth weight) in consideration of the uterine efficiency of unilaterally ovariectomised (ULO) does. Similarly, greater emphasis should also be placed on the milk producing capacity of does. Litter weight at 21 days could be the criterion for selection, and selection could be performed simultaneously for quantity of milk produced and for milk composition.

Nutrition

In practice, among the results to be achieved in the future some of the most rapid may be anticipated from adequate nutrition of the doe. In circumstances of more favourable nutrient supply to the doe the degree of nutrient supply to the foetuses and suckling rabbits also improves with the condition of the doe. Based on the processing of a large quantity of literature data MAERTENS (1992), XICCATO (1996), FORTUN-LAMOTHE (1997) and ROMMERS *et al.* (1999) all presented an outline of the results achieved from this aspect within the field of nutrition. Many encouraging findings have been made in connection with increase in dietary energy level and also in relation to sources of energy. In some instances an increase in birth weight has been accomplished; in a number of cases improvements of between 7 and 14 % in doe milk production have been achieved, while the weaning weight of the offspring has also risen by a similar proportion.

One of the most important areas of research for the future could be early direct feeding of young rabbits. Although young rabbits can also be reared artificially, almost entirely without a doe, this procedure has very limited practical feasibility. The expectations of the 'starter kit diet' were summarised in part by MAERTENS and DE GROOTE (1991), who emphasised the role of fibre and energy (i.e., fat). So far no success has been achieved with the various forms of milk substitutes available (BLAS *et al.*, 1990; CHMITELIN *et al.*, 1991; FERGUSON *et al.*, 1997). Endeavours should be made to find a means of ensuring that suckling rabbits are able to switch to solid feed at an earlier stage.

A technical concern in the solid feeding of young rabbits is that a solution to the problem of feeding the doe and her suckling offspring separately needs to be found. However, indications have been detected that the doe incites the young to eat and drink (MAERTENS and DE GROOTE, 1990).

One of the potential techniques which could be applied to ensure that suckling rabbits become accustomed to eating solid feed at an early stage is to wean them very early (SCHLOLAUT and LANGE, 1971; FERGUSON *et al.*, 1997; PIATTONI and MAERTENS, 1999; GYARMATI *et al.*, 2000; SZENDRŐ *et al.*, 2000). However, early weaning is accompanied by many concerns related to digestion physiology (decrease in gastric pH, production of digestive enzymes, development of intestinal flora and caecotrophy, etc.), housing and welfare.

Fostering

The fostering into smaller litters of rabbits born in larger litters is a long recognised procedure used in practice. A number of accounts of the various methods of fostering have been published (ROUSTAN *et al.*, 1980; LEBAS and DORCHE, 1982; PLA and MAHO, 1988; TORRES, 1988). Where systematic fostering has been used for the purpose of ensuring that all litters contain 8 suckling rabbits pre-weaning mortality has been reduced to 5.1 % in post partum breeding does (MAERTENS *et al.*, 1988). Where simple fostering is used the greatest problem is that in most cases animals of lower weight from larger litters are introduced into smaller litters where the other young are heavier. This puts the fostered rabbits at a disadvantage in the struggle for the teat (i.e., for milk), which results in great differences in weight within the litter.

A paper by POIGNER *et al.* (2000) drew attention to the significance of intra-litter homogenisation of weight. In one of the experiments in this study litters were formed with 6, 8 or 10 rabbits of different birth weight in equal ratios (39-70g). In the other experiment litters of the same sizes were formed, each consisting of rabbits of a single weight group only (small, medium or large). With increasing birth weight and decreasing litter size mortality among the young decreased, and the daily weight gain of the kits and their weight up to 10 weeks of age increased. Intra-litter homogenisation of birth weight markedly reduced mortality among the young rabbits and SD in live weight within litters.

Intra-litter homogenisation in rabbit breeding sites is often performed at birth, but in some cases weight within litters is balanced during the suckling period. The application of this method serves the purposes of reducing mortality and balancing out weight differences within the stock. However, an aspect not to be neglected is that small rabbits are saved to the detriment of the larger ones, as there is no change in the milk production of the doe: the milk is merely distributed 'more fairly' among the young.

Double suckling

An entirely new possibility was presented by HARMAND *et al.* (1970), SPENCER and HULL (1984) and SPENCER *et al.* (1985) when they reared young rabbits with two does in order to model overfeeding in human infants. MCNITT *et al.* (1988), SZENDRŐ *et al.* (1998) and GYARMATI *et al.* (2000) have constructed and run similar experiments.

From the findings of the above studies it can be established that young suckling rabbits are indeed willing to suckle from two does, one in the morning and the other in the afternoon (or evening). Milk intake in young rabbits suckling twice daily has been found to be 84 to 89 % higher than ones suckling only once a day, and those nursed twice daily have been found to gain weight more rapidly (MCNITT *et al.*, 1988; GYARMATI *et al.*, 2000). Weight gain in the first three weeks of life has proven to be 86 to 92 % greater than in young rabbits reared in the traditional manner. The absolute difference in body weight which developed remained even after weaning; indeed, due to the higher feed intake characteristic of double-suckled rabbits after weaning this difference actually increased, and thus these rabbits reached slaughter weight 8 or 9 days sooner than those which had suckled only once a day.

These findings draw attention to the degree to which the quantities of milk produced by rabbit does fall short of the actual requirements of suckling rabbits, and highlight the fact that for this reason the young are unable to express their genetically determined capacity for growth.

The above results were obtained by the process of selling or fostering the litter produced by one of the does used for double suckling. Thus, two does which had produced litters at the same time reared one litter between them. This procedure is not suitable for application in practice. Therefore endeavours have been made to devise potential techniques which would enable litters to be reared by two does without the need to abandon one of the two litters produced. After experimentation with a number of possible methods, the most favourable results have been achieved where a doe whose litter had been weaned at the age of 21 or 25 days was used for the second suckling (SZENDRŐ *et al.*, 2000 a,b). In both cases (i.e., after weaning on either date) the young had access to substantially greater quantities of milk: their weight gain in the first weeks of life improved and the final result was that they reached the slaughter weight of 2.5 kg 5 or 6 days sooner.

Further experiments are required for the purpose of examining how the double suckling procedure influences the milk production of does.

In conclusion it can be established that the knowledge available to us at present provides no substantial possibility for reducing maternal effects emerging in foetal life and manifesting itself in the weight of foetuses and newborn rabbits. On the other hand, double suckling or other similar methods can enable the influence of the limited milk production of the doe to be reduced substantially.

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