

GENETICS OF THE RABBIT FOR WOOL AND MEAT PRODUCTION (1904-1987)  
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FIRST PART : ANGORA RABBITS' BREEDING AND GENETICS

Not much attention has been paid to the genetics of Angora rabbits at international conferences in the past. In an attempt to fill this gap we propose a synthesis of the available works written on the subject. The results of experiences reported in a sample of chosen published articles will be presented after pin pointing the centres of production of Angora wool in the world. The synthesis in itself shall be made to begin with a few notes on the typical physiological features of rabbit fur. The factors influencing the quantity of wool produced will next be considered together with a final assessment of the different breeds of Angora rabbits taking into account their capacity of reproduction ; that is, their fertility and prolificity rates. Finally, the implementation of a number of programmes is to be found aiming at improving specific genetic traits of Angora rabbits.

I - INTRODUCTION

It was very difficult to put a definite figure on worldwide production of Angora wool. Data obtained from different sources allowed for an estimate of a total production ranging between 8 and 9 thousand tons during 1986. China was by far the most important supplier with a production of between 7 and 8 thousand tons a year. Its production rose steadily towards the end of 1950s, but it did not attract much attention. China exported a considerable portion of its Angora wool, which could be described as thin, soft and short. It was obviously the case of wool obtained primarily from young animals before they were slaughtered for meat production. A long way behind came two South American countries : Argentina and Chile, respectively with 500 and 300 tons a year. Both of these countries maintained a close contact on a technical and economic levels with West Germany. This was also the case for Hungary and Czechoslovakia, with 180 and 150 tons a year respectively. Although production in France was only of about 200 tons a year, its Angora wool stood out for being long and bristly, gathered by plucking. West Germany itself must obviously be mentioned because, although its production only reached 20 tons a year, it played a very important role from a technical point of view. West Germany hosted about a thousand farms which stood out for their modest sizes with an average of 20 rabbits each, breeders being no more than amateurs in most cases. They resulted being members of local associations with their own experts (Rougeot et Thebault, 1984a) and rabbits were periodically sent to regional testing centres. The wool of German rabbits was long and soft, gathered by shearing. Thousands of pedigree sires were exported every year for reproduction purposes.

The synthesis was based on the consultation of 54 articles, in addition to those presented at this conference. Table 1 supplies additional information summarised according to theme and country. Most articles were supplied by only four countries ; that is, West Germany, Chile, China and France. The specific selection of material chosen confirmed the special role of West Germany among countries boasting much bigger productions of Angora wool. "Le Lapin Angora, sa toison et son élevage" (Rougeot and Thebault, 1984 a) ["Angora rabbits, fleece and breeding"] was a useful source of information and shall indeed be quoted at several instances.

II - THE ANGORA RABBIT : ITS FLEECE

A. Physiological features (Rougeot and Thebault, 1984 a).

Rabbit coats are made up of three different kinds of hairs : bristles, awns and downs. The coats of Angora rabbits still present the typical composition of their peers which did not undergo any mutation. Their structure was simply modified by the three kinds of hair being much longer. Hairs are easily identified and allocated to the appropriate category (table 2) according to their length and diameter. It was possible to discriminate a subclass within hairs ranked as bristles, known as tylotriches

hairs. Bristle hairs present well defined heads resting in a downward looking position. They are the longest and most resistant of the three types of hair. Awn hairs also present relatively thick heads contrasting with their thin body. These two types of hair, bristles and awns, form together what is defined as guard hairs since they provide a sort of protective barrier. Down hairs are to be found close to the skin, acting as insulators, and are not usually endowed with heads. Each bristle hair can boast between 50 and 60 downs that form the undercoat or fur.

The growth period of the different types of hair is precisely the same, regardless of their nature, in a given coat. It was then reasonable to deduce that resulting differences in length were the outcome of differing growth rates. In all mammals, except for sheep, hair follicles work on a cyclical pattern made up of a period of activity or anagene followed by a period of rest or telogene. The periods of inactivity are not always as stable and predictable as the periods of activity, the length of which varies according to the type of hair the follicles are meant to supply.

The distribution of hair follicles on the skin is not determined at random, they are on the contrary assembled in homogeneous functional unities, known as follicle groups. In fact, while some hair follicles are specialised in the production of guard hairs, others supply down hairs. The type of hair produced is determined by the place of the follicle in its group. The age at which the follicle was formed determined its place in the group. At first, there is a succession of 4 or 5 generations of central primary hair follicles. Subsequently, two lateral primary follicles get established on each side of every central primary follicle with a resulting pattern of a very wide angle. Secondary follicles will establish themselves afterwards within the previously defined area. Their formation was the result of a proliferation of pre-existing hair follicles. The follicle group specific to rabbits is made up of a central primary follicle for the production of a bristle hair each, four lateral primary follicles for awn hairs, and a bundle of secondary follicles for down hairs (table 2).

#### B. The Angora mutation

As it was the case for mice (Pennycuik and Raphael, 1984), an extension of the active phase in hair growth (anagene) was at the origin of the unusual length of the coat of Angora rabbits (Rougeot and Thebault, 1984 a and b). After Angora rabbits, similarly to rabbits which did not undergo any mutation, were plucked, the growth rate of hairs increased steadily for the first 3 to 5 weeks. The growth rate became steady after it reached a maximum pitch, which was determined by the final length of the hairs in questions ; that is, the longer the hair, the higher the pitch. While hair growth stopped suddenly at the sixth week with rabbits not presenting any mutation, complete hair growth took more than thirteen weeks with Angora rabbits. The Angora mutation did not however prolong the duration of the active phase (anagene) according to any regular pattern. Some hairs completed their growth cycle at the end of six weeks and were shed while others were still growing at the end of 5 months.

Rougeot and Thebault (1984 a) reported to have obtained bristles as long as 40 cm. Choosing the moment to harvest Angora wool is a matter of compromise and it is usually carried out when a relatively small proportion of hair (10 % to 30 %) has reached its inactive period (telogene). It appeared possible to increase the average duration of the anagene phase with an appropriate selection programme. Rougeot and Thebault (1984 a) suggested that this is what happened with the strain selected for shearing. They even put forward the hypothesis that German Angora strains may have adopted the same process that allowed regular growth of wool in sheep to become a permanent feature.

The Angora character is due to a pair of autosomal and recessive genes. Mirgiyans (1973 a and b) carried out crossbreeding between some Angora rabbits with down hair measuring 62 to 72 mm. and some Rex rabbits with down hair of 18 to 23 mm. The first generation of interbred offspring produced down hair the length of which was within 29 and 33 mm which was the equivalent to the coats of rabbits not presenting any mutation. The second generation of interbred offspring presented either an Angora coat or a Rex coat or a coat lacking mutation. These three phenotypes appeared in ratios of 4, 3 and 9. It is quite surprising that Mirgiyans came to conceive the existence of some kind of complementary genes. Rougeot and Thebault (1984 a) carried out the same cross-breeding experiment. The frequencies phenotypes were present at the second generation (the actual results were not published) seemed to confirm the hypothesis of the 2 autosomal recessive genes. According to Fox (1986) the Angora gene belonged to the second linkage group with the Dutch pattern (recessive white spotting) and the English pattern (dominant white spotting).

### C. Pleiotropic effects of the Angora gene

Several researchers (Bedekar et al., 1984 ; Damme et al., 1985 ; Munsel et al., 1982 ; Sinkovics et al., 1979) compared litter size and adult live weight of Angora rabbits with that of rabbits which did not undergo mutation. On average Angora rabbits reported medium scores on both aspects. Nevertheless their specific features did not seem attributable to only the Angora gene. With reference to the analysis presented earlier with regard to the Rex gene (Rochambeau and Vrillon, 1986), two hypotheses were feasible. First hypothesis : the features were due to a pleiotropic effect of the gene examined. Second hypothesis : the remaining portion of the Angora rabbit genome was responsible for specific features. Angora rabbits have been selected for several generations mainly for wool production. It is nonetheless noteworthy that with regard to sheep the fertility rate of the strains selected for wool production did not diminish significantly (Haresign, 1983). At the same time, hardly any attention was paid to improving Angora rabbits' live weight, and a counterselection was occasionally practiced against big litters. That was the case in France where breeders used to dispose of newly born rabbits immediately at birth as does were reputed unable to raise adequately litters of more than 5 or 6. It also appeared probable that for a given trait determinism combined the two hypotheses in accordance with a pre-established pattern. Therefore, features of Angora rabbit fleece were determined mainly by the Angora gene, but also by the remaining genome of this breed. Damme et al. (1985) studied the growth of New-Zealand white, Angora and crossbred rabbits. The crossbred samples reported a live weight close to that of New-Zealand White, which seemed to support rather the hypothesis of the pleiotropic effect of the Angora gene. To decide definitely between the two hypotheses the gene examined, the Angora gene in this case, would need to be active in a number of different genomes. A programme of backcrossing allowed precisely this type of analysis with regard to the Rex gene. An equivalent study on Angora rabbits could well provide interesting information. To fully benefit from a programme of genetic improvements, it would be useful to know whether the low level of fertility of Angora rabbits was due to a pleiotropic effect of the gene or due to the remaining portion of the genome. In the latter case a fertility programme of selection would present even more interest. The low levels of fertility must be considered in relation to the current practice of delaying reproduction until very late in the life cycle of Angora rabbits, and to the very considerable extensive nature of the rhythm of reproduction employed.

### III - ANGORA RABBITS' WOOL PRODUCTION AND THE FACTORS IT IS INFLUENCED BY.

#### A. Wool harvesting cycles and harvesting methods.

Angora wool is gathered either by shearing or plucking. The latter method is used especially in France. According to Rougeot and Thebault (1984 a) plucking did not affect the behaviour of hair follicles, and the hairs of Angora rabbits continued to grow in appropriate synchronism obeying to the rhythm typical to each type of hairs. On the contrary shearing did not appear to encourage hairs to grow. What happened was that, while some hairs followed their established growth programme, others started their growth cycle randomly. There were two important consequences derived from this absence of synchronism. Coats were less well structured since hairs were cut at different stages of their growth giving the coat a wooly look. Shearing also left the replacement of coats exposed to a greater degree to seasonal influences. There seemed to exist a higher share of fully grown fleeces at the beginning of spring, summer, autumn and winter. Obviously breeders should preferably carry out their shearing in these periods.

Rougeot and Thebault (1984 a) recommended French breeders to wait until their Angora rabbits were 8 weeks old before plucking them for the first time. The next harvest was to take place 13 weeks later; that is, at the age of 21 weeks. Afterwards the rabbits were plucked at intervals of 14 weeks. Some breeders only leave 13 weeks between pluckings, which was also the length of the intervals chosen by German breeders. In Chile Garcia and Magofke (1982) adopted a slightly different pattern with the first shearing taking place when the rabbits were 9 weeks old, the second 20 weeks old, and subsequent shearing at intervals of 10 to 11 weeks. It would seem that shearing allowed the adoption of a more sustained rhythm than plucking. The adoption of such a pattern would have the effect of increasing the quantity of wool harvested, but equally to a reduction in the length of the hairs gathered each time.

## B. Factors influencing wool quantity

First will be presented the factors which, although not of a genetic nature, gave an explanation to the degree of variability observed within the elements of the same farm. It is equally worth considering the age of the rabbit, whether it is male or female, its live weight, the precise months wool is harvested and the length of intervals between harvesting. The results will be presented in form of tables and an effort shall be made for the different contexts they were obtained from to become evident (level of production, shearing or plucking, ...). An analysis of the available genetic parameters shall subsequently be exposed.

### 1) Age and correlative harvests

The total weight of wool harvested increases rapidly during the first four harvests (table 3). Only at the fourth harvest the wool appear to reach a fully mature structure. The quantity produced continues to increase, but it eventually begins to fall. The period at which wool production was reported to be at its highest pitch varied from author to author. Rougeot and Thebault (1984 a) discriminated between adult does and old does without specifying the exact period of change. Thebault and Rochambeau (1988) studied the evolution of wool production up to the twelfth harvest. The level of production was at its highest at the seventh harvest, but these results were open to discussion since they were obtained exclusively from a selected sample. On the contrary Ocetekiewicz and Tuczynska (1981) observed that the level of production kept growing for at least the first three years; Ricke Munoz (1984) achieved his maximum production from the third harvest.

### 2) Sex

Bucks produce less wool than does (table 4). Magofke et al. (1982 b) established in a bibliographical analysis of their own that the differences in production ranged between 2% and 22%. It seemed that the higher the average production, the higher the differences between bucks and does as confirmed by the margins of 11% to 18% observed in Europe and the United States on highly productive animals. These margins became even more evident in winter. Estimations based on the results of German testing centres fluctuated between 10% and 15%.

Rougeot and Thébault (1984 a) estimated the fairly higher percentage of 20%. This could well be related to the fact that French breeders did not give much importance to the quality of bucks in their herds. On the contrary German breeders did and this undoubtedly created a bias in the estimation. It was suggested to castrate male Angora rabbits to compensate their handicap in wool production. Gomez (1981) quoted by Magofke et al. (1982b) achieved by this method a production higher by 7% to that of female Angora rabbit. Scholaut and Lange (1983) however reported that the production of castrated bucks was of an intermediate level.

### 3) Live weight and litter size

There is a close correlation between live weight and the quantity of wool harvested at the first harvest (table 5). Its importance appears to decrease afterwards. Jelinek et al. (1980) reported a phenotypic correlation of 0.58 for bucks and 0.41 for does at their 2nd and 3rd harvests. Magofke et al. (1982) quoted the following values based on a bibliographical survey: 0.39 for rabbits 6 months old; 0.25/0.30 for rabbits 14 months old; 0.18/0.23 for adult rabbits. They also supplied the genetic correlations for the first three harvests: 0.62, 0.97 and 0.70 respectively. These evaluations were not however validated. Jelinek et al. (1980) classified their rabbits in 4 groups in accordance with their live weight. If the value of 100 is assigned to does weighing between 3410 g to 3700 g and producing 155 g of wool at their third harvest, the following indices are obtained: 77 for does weighing less than 3100 g; 86 for those between 3110 and 3400 g; 95 for those with a live weight above 3710. This simple analysis would indicate that rabbits were more productive the higher their body weight, while still keeping it within a reasonable threshold. Schley and Scholaut (1988) pointed out that in Germany taking the weight of wool produced per unity of live weight as a selection criterion resulted in the size of animals as well as the quantity of wool harvested being reduced. That is why the correlation with live weight was abandoned in 1972.

An analysis of the data of another German grading centre (Bayerische Landesanstalt, 1982 to 1987) established an increase in the weight of Angora rabbits (table 10). As it often happens the definition of live weight with adult rabbits is a complex matter. Thébault and Rochambeau (1988) observed that the live weight of French Angora does changed from 3826 g nine weeks before their 4th harvest to 4247 g nine weeks before their 11th harvest ; that is, an increase of more than 10 %. At the same time the weight of these same does fluctuated during the year with a negative variation with a minimum of (-5%) at the beginning of summer, and a positive one at the beginning of winter with a maximum of (+5%). Charlet-Lery et al. (1985) reported equivalent seasonal changes. They however pointed out that among the 9 does under observation, the highest production of wool came from those which consumed the lowest quantity of feed and did not put on weight during the year long experiment. Indirect selective procedures based on live weight would not be as effective as Garcia and Magofke (1982) presumed.

With regard to sheep the correlation between fleece weight and the animal's live weight is variable (from -0.3 to 0.6). Selection experiments aimed at increasing the weight of fleeces tended to reduce live weight. On the contrary, selection procedures aiming at increasing live weight provoked a rise in wool production. (Haresign, 1983). To draw a complete picture, the existence of a highly negative genetic correlation in the case of Cashmere goats was remarked (table 9) between fleece weight and animal's weight at the age of 18 months (Milliar, 1986). This correlation would indicate that body growth was antagonised while the growth of the coat was going on.

Magofke et al. (1982b) approached the problem from a different perspective and studied the influence of litter size at birth on wool production (table 6). Differences in live weight were very prominent at weaning (up to -37% in relation to animals of smaller litters) and assumed a certain importance at the time of the first harvest (up to -18%). Although significant, they remained under 10 % afterwards. The weight differences of fleeces were significant only for the first 2 harvests, even if animals born in litters of more than 5 always reported a production 5 % lower at their 4th harvest. Animals born in big litters partially compensated their production handicap derived from a lower live weight. The results indicated both the existence of a limit to the litter size a doe's suckling capacity could cope with and the complex nature of the connection between Angora rabbits' fleece weight and live weight. Despite the values of the correlation coefficients, a linear correlation would only present part of the real picture.

#### 4) Seasonal influences

Winter harvests are more productive than summer ones. To complete table 7, it is necessary to quote the bibliographical studies carried out by Magofke et al. (1982b) and Rougeot and Thébault (1984). In the first case the observed seasonal differences in wool production varied between 7 % and 44 % ; in the second case they were between 3 % and 51 %. It appeared that the summer fall in wool produced tended to decrease as the level of production rose and in proportion with the age of the rabbit. The data obtained by Thébault and Rochambeau (1988) seemed to show that quite clearly. It must be nevertheless pointed out that important differences persisted even with adult rabbits when it was the month rather than the season that was considered with regard to harvesting. In the case of an average production of 242 g, the coefficient for January's harvest was 107 while that of August was 95 (Thébault and Rochambeau 1988). These seasonal variations were due to variations in the photoperiod (Rougeot and Thébault, 1984 a and b). Histological analyses revealed that part of hair follicles disappeared in spring (-12%) and even more in summer (-28%). Only secondary hair follicles derived from epidermal follicles were affected which would germinate again in autumn.

Seasonal moulting is controlled by photoperiodism which act on hormone balances. At present only 2 hormones are known, prolactin and melatonin, to act on moulting. Implants of melatonin permitted to do away with the summer fall in wool production (Rougeot, 1986).

#### 5) Intervals between harvesting

It is important to take this factor into account especially when there is a need to compare results obtained from different breeding stations. That is to say, for example, that a rabbit producing 300 g of wool every 16 weeks does not add up to 1200 g a year, but rather 975 g.

Intervals between harvesting are usually kept constant in experimental protocol which would explain why Magofke et al. (1982 b) did not treat it as length when it was used as covariable of the fluctuations in fleece weight. The effect of this covariable was significant for 1st, 2nd and 3rd harvests where the regression coefficients corresponded to 0.47 g, 1.31 g and 0.79 g relative to average productions of 27 g, 114 g and 144 g respectively. The limited degree of variability of the interval leading to the third harvest was taken to account for it not being significant.

Jadrijevic et al. (1982) carried out an experiment in which rabbits were sheared according to a programme of variable intervals between 10 and 70 days. The group of animals sheared at intervals of 20 days reported the highest rate of wool production per day (2.56 g per day). The rate of production fell as the length the intervals increased. The rabbits on intervals of 70 days only reported a production of 2.12 g per day (-17%). These results showed why certain breeders tended to make use of relatively short intervals between 2 consecutive shearings. However, it is necessary not to neglect the quality of wool produced, notably its length. As Rougeot and Thébault (1986 a) pointed out, choosing the moment to carry out shearing is a matter of compromise.

#### 6) Connections between quantity of wool harvested and genetic parameters

There seem to exist only two series of genetic parameters being estimated in the case of Angora rabbits. Garcia and Magofke (1982) obtained poor estimations for the first 2 harvests and even poorer for the following two (table 8). They however pointed out that their results agreed with Bettini's (1952, quoted by Garcia and Magofke, 1982) who attributed a degree of heritability hardly worth considering with regard to first year's fleece weight. Their estimations for subsequent years were on the contrary in the region of 0.75. Garcia and Magofke's (1982) estimations of heritability with regard to live weight appeared to fluctuate constantly from one harvest to the other. The available estimations for other species of domesticated mammals will help to complete the picture drawn on these contradictory results. In the case of Cashmere goats (table 9), heritability of undercoat weight was around 0.50 (Milliar, 1986). In the case of sheep, estimations of heritability of the fleece weight varied between 0.30 and 0.40 (Haresign, 1983).

#### C. Factors determining fleece quality

##### 1) How fleece quality was defined ?

The French Angora Trade Association (Syndicat National Angora Qualité) outlined 5 categories of wool (Rougeot et Thébault, 1984a) :

- 1st selection, grade A : clean, long (above 6 cm), bristly wool ;
- 1st selection, grade B : clean, long (above 6 cm), woolly wool ;
- 2nd selection : clean short wool ;
- clean felted wool ;
- dirty wool.

In all countries the quality appeared being worked out very much alike with length, cleanliness and absence of felting constituting their classification criteria. Thébault and Rochambeau (1988) put forward 3 quality criteria of their own : homogeneity, structure and tautness. Homogeneity was calculated as the ratio between the weight of quality A1 wool and total weight of the fleece. Structure was analysed as the ratio between the length of downs and that of bristles. The appreciation of the wool's tautness was regarded as the result of a subjective opinion following an examination by the feel. These 3 criteria were included in the French Angora Trade Association's grading checklist.

##### 2) Differentiation factors

Initial harvests were exclusively made up of 2nd selection wool. At the second harvest, 1st selection wool was present, but it was not adult wool yet. It was possible to allocate the wool gathered at the third harvest to the different categories just like adult wool, but the quantity produced was less. The first true adult production took place at the fourth harvest (Thébault and Rochambeau, 1988).

Angora wool was reported to be shorter in summer than in winter. The difference in length was more evident with downs than bristles, which lightly modified their structure. Rougeot and Thébault (1984 b) estimated this reduction in length at 10 % for bristles and at 17 % for downs. Thébault and Rochambeau (1988) provided slightly lower values and suggested that winter fleeces were more homogeneous than summer ones. Bucks presented a lower percentage of wool its length being above 6 cm than does (63 % versus 72 %). However, as does got older the homogeneity of their fleeces decreased slightly together with their structure and tautness (Thébault and Rochambeau 1988). By the way, the degree of impoverishment in wool production was not so significant as Garcia and Magofke (1982) feared. As a matter of fact, the variations found in hairs' thickness were minimal (Rougeot and Thébault, 1984 b ; Jelinek et al., 1981). Other researchers carried out studies on other Angora wool features such as fibres' breaking resistance or elasticity (Raichev and Damyanova, 1980 ; Jelinek et al., 1981). The correlation between the presence of quality features and fleece weight was positive or not significant, except for tautness (phenotypic correlation equal to -0.23, Thébault and Rochambeau 1988). In the case of Cashmere goats (table 9), length and diameter of their undercoats seemed undoubtedly correlated to total weight, that was not the case for diameter. The achievement of a simultaneous increase in undercoats' weight and length together with a decrease in hairs' diameter would be a difficult goal. With regard to sheep, features determining quality in fleeces appeared to be moderately to highly hereditary and showing a positive link with the fleece's weight (Haresign, 1983).

#### IV - GENETICAL EVALUATION OF DIFFERENT BREEDS

##### A. With regard to wool production

Thébault and Rougeot (1984 a) resumed the evolution of Angora rabbits' productivity in France. They assessed for 1920 an annual production of 200 g per rabbit, 450 g for 1940, 480 g for 1950, 650 g for 1960, 840 g for 1970 and 1000 g for 1980.

Centres testing and keeping a record of Angora wool production could be found in West Germany. The evaluation of annual averages outlined interesting results. With regard to the centre at Ulrichstein, the data available covered as far back as 1934 (Schley and Scholaut, 1988 ; Scholaut, 1987). At that time annual production was estimated at 400 g per rabbit. In 1959 it was around 700 g for does. For the following 10 years the annual increase was of about 32 g a year ; that is, an overall rate of 3.6 %. In 1969 the annual production per doe amounted to about 1100g. During the subsequent 10 years the increase was a lot less remarkable : 17g a year ; that is, an overall rate of 1.5%. In 1979 average production was about 1200g. Since that year the upward trend in production picked up speed ; 32g a year ; that is, an overall rate of 2.5%. In 1985, the average production of does tested at the centre exceeded 1400g.

The records of another centre (table 10) were also interesting. The production of a particular doe was assessed as stagnant or even regressing (-10g per test) and it seemed to outline a general tendency for does to increase their live weight (+80g per test).

Schley and Scholaut (1988) rightly pointed out that the conditions in which testing was carried out had altered several times over the years. Improvements in environmental conditions have taken place, in particular, the introduction of complete granulated feed was a great progress at the nutritional level. It became clear enough that the data was not sufficient to calculate any genetic progress as it could not be taken as a representative sample of the average Angora rabbit population in Germany. It simply stated the potential of the German breed.

Productivity was reported to be at times at much lower levels. In Chile, Magofke et al. (1982) obtained 429g of wool the first year with rabbits weighing 3300g. In India, Singh and Negi (1986) assessed their annual production at 260g with rabbits weighing 2300g.

It was quite surprising that rather little breeds comparison was available (table 11). According to data supplied by Garcia et al. (1984), German bred rabbits were slightly superior compared to rabbits of a local breed in Chile. There was no trace of an heterosis effect. On the contrary, Gao et al.

(1983) found noteworthy differences between a German breed and a local Chinese breed. Three generations of back-cross breeding doubled production. Dai et al. (1985) carried out a comparison between German and French animals. The German breed turned out much more productive. Heterosis effects were low (8%). It would be desirable for German, French, Chinese and Chilean breeds to be compared between them in the shortest possible delay.

## B. Fertility and fecundity

### 1) Fertility in bucks and does

The quality of the sperm of Angora rabbits was studied by several researchers. Brockhausen et al. (1976 and 1979) proved that it was not influenced by the length of their fleece. There were no differences reported between Angora bucks and bucks whose coat had not undergone mutation. Yan et al. (1985) observed the influence of an increase in the surrounding temperature in sperm's production and quality. They reported a disastrous effect. Hu et al. (1983) pointed out that while the percentage of abnormal spermatozoa doubled in summer with German bred bucks (23% vs 50%), it remained at much lower levels with bucks of a local Chinese breed (17% vs 27%).

In a comparison operation between Angora does and does which did not undergo mutation, Sinkovics et al. (1983) were able to establish that the former bore poorer fertility rate (45% versus 75%). Angora does inseminated immediately after shearing reported a fertility rate ranging between 46% and 70% depending on which day the insemination was performed. Thébault and Rochambeau (1988) observed poorer fertility rates from natural mating : 25% per mating or 52% between consecutive harvests.

### 2) The fecundity rate of does

Litter size at birth appeared low (table 12). It seemed to be the result of a high rate of embryonic mortality (Brockhausen et al., 1979). The first ovulation rates being estimated by us (results not yet published) indirectly confirmed these mortality rates. According to Garcia's et al. results (1984), direct heterosis on litter size at birth was very important (above 30%). Despite the reduced litter size at birth, the likelihood for the newborn rabbits of living at weaning was low. An Angora doe's capacity to foster appeared limited with regard to litter size. That was why French breeders carried out a selection at birth according to sex and only newborn does and a few bucks were kept (Rougeot and Thébault, 1984). For example, in the case of does who fostered 4.9 live borns, its litter would be reduced to 3.18 newborn rabbits : 0.89 bucks and 2.29 does (Thébault and Rochambeau, 1988). This type of limitations also appeared clearly in Garcia's et al (1984) data. Direct heterosis which had been of +34% in relation to litter size at weaning was only of +13% in relation to litter total weight at weaning.

### 3) Demographical parameters

Knowledge of a population's demographical structure should be regarded as an indispensable prerequisite for the elaboration of a genetical improvement programme. So it may come as a surprise to discover the limited availability of references on the subject. Rougeot and Thébault (1984 a) estimated an annual replacement rate of about 25% in French Angora farms. In a herd of 100 does demographically balanced it would be sufficient for 5 days to raise two litters a year with 2.5 new does in each of them to maintain a constant rate of replacement. If the farm of Angora does was sectioned according to age in one year differences, its age distribution would be : 24, 22.5, 20, 16.5, 11, 5, 1.25. That is to say that for 100 does, there would be 24 one year old does, 22.5 two year old does...

Thébault and Rochambeau (1988) assessed the demographic parameters of an experimental Angora herd. The results showed two outstanding differences with regard to the estimations presented above. Mortality rates were higher : 25% of does of the cohort under examination disappeared each year during the first three years. Because of this more significant rate of natural selection and because of a poor fertility rate, two thirds of does in the cohort had been mated at least once, and half of them had raised at least one litter. Even if these data were obtained in experimental conditions, it was likely that the elimination rate of live-stock in France's average Angora farms was higher than Rougeot and Thébault (1984 a) believed. It would appear that the turn-over rate in Chile was higher according to Ricke Munoz (1984) who estimated a 21% mortality rate between consecutive shearings. Garcia and Magofke (1982) formulated a model in which the life span of its rabbit population did not exceed 2 years.



Rochambeau et al. (1988) described French Angora rabbit reproductive life. The reproductive life of the rabbits in the Herd Book started as they were about 20 months old. It lasted for an average of 13 months for bucks and 8 months for does, corresponding respectively to 8.6 and 1.8 litters. 20% of bucks and 33% of does only produced one litter. Does' average age when they gave birth to their first litter was 12 months in this experimental herd and in some herds observed in the Herd Book. 80% of litters were born between the 3rd and 8th harvests on the doe side. In the Herd Book the gap between generation was of 22 months calculated starting from the cohort of descendants born in 1984.

It seemed that these Angora rabbit populations presented demographic features which were more in common with sheep than with rabbits reared for their meat.

#### V - PROGRAMMES OF GENETIC IMPROVEMENTS

Apart the genetic programmes set up in West Germany and France, there did not seem to be much work published on the topic. The models worked out by Garcia and Magofke (1982) as well as that of Singh Yadav and Dempfle (1988) deserved nevertheless mentioning. But the degree of reliability of the results obtained from these two simulation remained questionable since the demographic and genetic parameters of Angora rabbit populations were largely unknown.

##### A - Angora rabbits' selection procedures in West Germany

Rougeot and Thébault (1984 a) described the scheme applied in Germany where breeders were often fancy breeders. Selection schemes were based on the performances recorded on animals which took part in a large number of competitions. On a local level records were kept starting from a minimal age of 4 months. Animals were checked for one year; that is, 4 harvests taking place 3 months from each other. Wool value was calculated taking into consideration the weight of the different categories of wool and subsequently working out a ratio according to total skin surface. Bucks' wool value was increased by 20%. A mark was given to this wool value. If the parents and grand-parents of a rabbit held their performances on record, the mark adjudicated to their wool value was added to the rabbit's own mark. 100 was the highest mark. Rabbits were then scored. Out of a total of 100 marks, 20 were assigned for fleece compactness and homogeneity, 15 for wisp structure, 40 for physical development and 25 for standard features. The sum of these two marks gave the final value assigned to a single rabbit. The latter ones were distributed in five classes according to the nature of the available information about the animal under observation, plus possibly its parents and grand-parents.

Breeders could also have their rabbits graded in regional testing centres. Schley and Schlolaut (1988) outlined a historical account and present modalities of operation of these centres. Since 1984 the animals were kept under observation for three months prior to shearing. They were reared within an enclosed building on a complete granulated feed. A year long wool production was worked out, basing all calculations on the weight of the wool harvested under these experimental conditions. It was then possible to obtain the quantity of nourishment needed to produce 1 kg of wool, the distribution of the wool among the different categories, as well as the animals' live weight at the end of the test. To conclude, Schley and Schlolaut (1988) made six remarks :

1. too much importance must not be assigned to standards ;
2. selection of a breed with multiple medullated hairs would attract a certain interest ;
3. fertility rate must not be neglected ;
4. rational utilisation of bucks in artificial insemination should permit to accelerate progress and to better estimate genetic values ;
5. subjective judgements on length and percentage of multiple medullated hairs must be replaced by objective measures ;
6. absolute results obtained from a breeding centre or farm meant very little, only comparisons hold informative values.

German bred Angora rabbits were internationally well reputed and German breeders exported every year several pedigree sires for reproduction.

B - Selection of Angora rabbits in France (Rougeot and Thébault, 1984 ; Rochambeau et al., 1988)

French breeders were divided into two main categories, one of which was made up of farmers for whom the rearing of Angora rabbits only constituted a complementary activity, while in the other the rearing of Angora rabbits was the farmers' main source of income. The number of breeders have increased steadfastly since 1984 and the size of their herds was bigger than that of their German colleagues (an average 100-150 rabbits). A herd book was created in 1956 (The French Angora Rabbit Book), the setting of which was on the same lines as those dealing with other species of domesticated animals. Breeders sent a birth registration for each litter, the animals were subsequently identified at weaning and graded prior to their fourth harvest. Breeders were to weigh the wool produced at each harvest and to report their results on the rabbit record card. Out of a count of 100 marks, 40 were for wool value, 40 for fleece quality (15 for homogeneity, 10 for structure and 15 tautness), 20 for physical development and 5 for head and ears development. The marking was carried out by qualified agents visiting all farms several times a year on behalf of the team compiling the herd book. The marking scheme permitted to achieve some important improvements both with regard to wool quantity and fleece quality. The introduction of computerised networks for the analysis of the data collected by the SNAQ constituted a new stepping stone as it enabled a better correction of environment effects, the formulation of more effective selection practices (selection carried out on relatives, the refining of selection criteria) and objectives (qualitative appreciation of fleece quality, reckoning with reproduction and growth, multicriteria index), and the maximisation of pedigree sires' circulation (valorization of bucks via artificial insemination...). The potential selection base existing in France suggested that swift genetic improvements were possible.

SECOND PART : GENETICS AND BREEDING OF RABBITS FOR MEAT PRODUCTION

At the time of world conferences on rabbit breeding Rouvier (1980) followed by Matheron and Poujardieu (1984 a) presented a synthesis of works carried out on the genetics of rabbits as meat producers. In the meanwhile Baselga et al. (1982), Masoero (1982) and Matheron (1982) presented the information they were in possession of on genetic elements determining litter size and live weight at the 2nd World Conference of Genetics Applied to Livestock Production (Madrid, 1982). The present synthesis was intended to illustrate the works carried out since the last world conference by the inclusion of what was essential of the articles presented in Budapest at the session of genetics. Before being studied to improve their performance as meat producers, rabbits have been, and still are, employed as animals for laboratory experiments. Useful information was obtained from these unrelated studies to be used in further research work on rabbits bred for meat production. Firstly, the knowledge acquired on this species, particularly with regard to its genome, will be exposed. Recent achievements in molecular genetics and immunogenetics will be found besides classical works on genetics. Secondly, the studies and comparisons between rabbit populations, and breeds will be synthesized. Thirdly, the techniques set to work and methods employed to achieve and promote genetic improvements will be analysed. Finally, an effort shall be made to answer some of the questions geneticists dealing with rabbits are faced with nowadays. These geneticists were often involved in the setting up of selection schemes and the promotion of genetic improvement policies. The analysis shall be carried forward with strict reference to the knowledge acquired in Western Europe (France, Spain and Italy above all).

The highest possible number of published works were assembled to compile this synthesis, amounting to about 300 pieces of work. They were grouped according to country and theme (Table 13). Rabbits were only partially dealt with in international bibliographical inventories. The main source of information was the material made available by the Commonwealth Agricultural Bureau, assisted by documents gathered by workers at the station. Nevertheless the present list does not claim to be exhaustive.

The 300 publications were divided into 10 themes. A portion of more than 20 % was devoted to comparing rabbit populations, and breeds; and a nearly identical number of publications dealt with methods of achieving and promoting genetic improvements. As it will gradually become clear, most efforts were directed to outline the applied aspects of research works. Each of three other themes took up an additional 10 % of publications, which dealt with either the study of a rabbit population or breed; or with the study of genetic mechanisms and parameters; and finally with immunogenetics. It will then be found with just under 10 % each, works dealing with genes and chromosomes; with genes producing visible effects; and with biochemical polymorphisms. So more than a quarter of publications were based on molecular biology. Lastly, there are two important themes defined as the presentation of selection experiments with rabbits and the presentation of technical results obtained from breeding farms. At the time of the conference in Rome, Matheron and Poujardieu (1984 a) regretted the limited availability of data from selection experiments. The situation having since improved, it was possible to index half a dozen selection experiments. Although it was important for scientists in applied genetics to gather information, all knowledge was meant to improve the operating of rabbit breeding farms. Therefore performance evolution at these breeding farms provided useful hints on the shortcomings of research works. Analyses of performances in breeding farms should be assigned a more important role in future conferences dealing with breeding of rabbits.

The way different countries were represented in the sample of publications was necessarily biased. Three distinct groups of countries became nevertheless clearly outlined. The first group included 6 countries with 20 or more publications. They were France, Spain, USA, Italy, USSR and Czechoslovakia. The three main producers from Western and 2 from Eastern Europe were present - Matheron and Poujardieu (1984 a) had already remarked on the considerable number of publications coming from Czechoslovakia. The distribution per theme of the publications supplied by the United States of America marked it well as a country where rabbits were regarded as animals more suitable for laboratory experiments than meat production. The second group (between 8 and 11 publications) brought together 5 other countries: West Germany, Belgium, Poland, India and Egypt. The importance held by each of these countries as rabbit meat producers differed considerably from each other, but they all had a common feature consisting of several teams carrying out independent works on rabbits in each of them. The third group (less than 6 publications) was made up of 18 countries and there was no doubt that for some of them, notably the People's Republic of China, the sample of publications chosen could not claim to give a true picture of the overall reality in these countries.

During the period taken into consideration 6 books dedicated to the study of rabbits were either published or new editions were introduced (Berestov, 1985; Cheeke et al., 1987; Lebas et al., 1984; Rudolph and Kalinowski, 1982; Schley, 1985; Stanford, 1986). It can be pointed out that Lebas's et al. work (1984) published by FAO, was available not only in French but also in English and Spanish.

#### 1. KNOWLEDGE OF THE SPECIES AND ITS GENOME

Knowledge in molecular biology has been developing rapidly for several years. Although mice remain the mammal most highly employed in experimental work, a few teams began to experiment on rabbits. Techniques such as electrophoresis considerably extended the achievements in classic genetics. After an examination of the works dealing with genes producing visible effects and biochemical polymorphisms, it shall be necessary to consider works on chromosomes and gene maps, molecular genetics and immunogenetics. Finally, mention shall be made of attempts to transfer genes between rabbits.

##### A. Genes producing visible effects and biochemical polymorphisms.

24 publications covered this theme. The important contribution of the Spanish team from the Faculty of Veterinary of Zaragoza deserved being mentioned.

### 1) Genes producing visible effects

Genes in charge of staining functions in rabbits were fairly well known, even if it was hard at times to explain the phenotypic effects observed in breeding farms. Several authors synthesized available information (Arnold, 1984 ; Fingerland, 1985 ; Lukefahr, 1986 ; Pape, 1986). Arnold (1984) managed to establish a correspondance between Anglosaxon symbolism, German symbolism and the most important rabbit.

During the period examined the other genes producing visible effects had not been thoroughly studied, except for those connected with coat production. Vrillon et al. (1988) described the exact nature of the Rex mutation. This mutation seemed to cause a degeneration of primary hair follicles and first generation of secondary hair follicles. This degeneration gave rise to an almost total disappearance of bristle hairs. Rochambeau and Vrillon (1986) studied the pleiotropic effect of this mutation on litter size and live weight in rabbits. An attempt was being made to introduce this mutation in the genome of a New Zealand White breed via a series of backcrosses. The results of these experiments will indicate the extent the limited litter size and weight of Rex rabbits was due to the mutation in itself and the extent due to the remaining portion of the genome. It shall be equally necessary to work out the interactions between genes and the genomes within which they operated. As it has been already mentioned, works of an identical nature were being carried out with regard to the Angora mutation.

### 2) Biochemical polymorphisms

An important polymorphism of a biochemical nature was revealed in several species by electrophoresis. The ZARAGOZA's team presented results obtained via electrophoresis at the Rome Conference. Several publications have since come about to further this initial achievement (Zaragoza and Amorena, 1985 ; Zaragoza and Arana, 1984 and 1986, Zaragoza and Zarazaga, 1984 ; Zaragoza et al., 1985, 1985 and 1987). Other works confirmed or completed the results obtained (Anderson et al., 1985 ; Kosaka, 1983 ; Varga et al., 1986). More than 15 blood proteins showing polymorphism were described in rabbits (Table 14). The genes which were responsible for these proteins were occasionally identified. Important polymorphisms with regard to the main complex of histocompatibility and immunoglobulins were identified.

Biochemical polymorphisms were good markers enabling to follow the history of rabbit populations and breeds. It was possible to work out genetic distances between different breeds (Zaragoza et al., 1987) and to estimate the degree of (Zaragoza et al., 1987). Varga and Palovics (1988) proposed to make use of these polymorphisms to carry out checks on parentage. They achieved a high identification probability rate of any 2 individuals through the 6 polymorphic systems used. But the operation resulted rather costly in relation to the value of the animals tested.

Desalvo and Zucchi (1985) studied a quantitative enzymic polymorphism and measured the quantity of 4 different enzymes present in the muscles of 4 rabbits. They highlighted differences between the breeds of New Zealand White, French Silver, Californian and Vienna Blue. But Chericato et al., (1985) were not able to achieve an equivalent success by studying metabolic parameters in rabbit blood.

There seemed to exist correlations between certain genetic markers and certain zootechnic performances in other species of domesticated animals. Gogeliya and Markovich (1981) would appear to have found a correlation of this kind.

### B. Genes and chromosomes

24 publications on molecular biology dealt with this theme ; they were supplied mainly by teams from the United States of America and the Laboratory of Cellular Genetics in Toulouse (France).

#### 1) Genetic chart of rabbits

A standardized karyotype of rabbits (*Oryctolagus cuniculus*) was adopted in 1981 and published in "Cytogenetics and Cell Genetics". Syntheses on genetics charts are compiled regularly (Fox, 1984 and 1987). At the time of the "Ninth International Workshop on Human Gene Mapping" (Paris 1987), a comparative study of the linkage groups in Man and in some species of domestic mammals was carried out. A Table was drawn up with the help of Geneviève Echard to synthesize the data from these three sources

(Table 15). More than 60 genetic markers were described in rabbits. They were either genes producing visible effects (coat colour genes, morphological anomalies, etc.), or genes coding for enzymes. These two different kinds of approaches met with difficulty, since teams often worked with only one type of markers. 37 markers were located in 8 autosomes and in X chromosome. 23 markers made up 6 linkage groups, but 6 markers had not yet been located. The totality of these markers could help to pick out a total of 22 pairs of chromosomes in rabbits. But possible correlations between enzymic markers and coat colour had been hardly tested. Articles dating as far back as 1933 and 1936 indicated that there appeared to exist 2 genes encoding the Rex mutation: one of German origin and one of French origin. A few years ago Rochambeau and Vrillon (1986) had the opportunity to crossbreed some Rex rabbits bred in Germany, Mexico and France. Realizing that all the animals obtained from this crossbreeding experiment bore a Rex coat, it was supposed that one of the two genes had disappeared.

#### 2) Additional achievements in molecular genetics

Certain genes in rabbits were particularly well known, such as the family of the beta-like globin gene. Hardison et al. (1981) compiled a bibliographical synthesis of available information with regard to the 4 genes in this family. The first was encoding a hemoglobin expressed in adult rabbits; the second constituted a pseudogene. The remaining two were encoding hemoglobins expressed in the embryo. These genes were sequenced (Hardison, 1981 and 1983) and their expression during development was examined in detail (Rohrbaugh and Hardison, 1983; Kavan and Ischenko, 1985). Several other genes were sequenced, such as the uteroglobin gene (a protein constituting an embryonic signal) (Bailey and al., 1983; Lopez de Haro and Nietto, 1985); the gene of a blood protein, the "reactive protein" (CRP) (Hu et al., 1986); the gene of another blood protein close to cytochrome P-450-1 (Johnson et al., 1987); and finally the gene of a muscle enzyme, the Phosphofructokinase (Lee et al., 1987). As far as it was possible to check at the time, these last 3 genes had not yet been located.

Also to be mentioned was a description of the mitochondrial ADN in rabbits (Ennaffas et al., 1987), the bringing to light of a certain type of repeated sequence in the genome of rabbits (Hardison and Printz, 1985), as well as the expression of heat shock genes in fetal and maternal brains of rabbits (Brown and al., 1985).

#### C. Immunogenetics

More than half of the 37 publications dealing with this topic came from the United States of America. It was nonetheless decided to limit our attention to a few publications on immunological mechanisms. No consideration was given to the many publications in which rabbits only appeared as producers of serum or as a laboratory animal used to study diseases such as experimental pulmonary candidiasis, experimental trichinellosis, experimental pulmonary aspergillosis, toxoplasmosis, etc...

A work team appeared to keep the public up to date with achievements in rabbit immunogenetics and immunology. It first got together in 1984 (Adler et al., 1984) and they planned to meet again in 1986. Among several syntheses, a work on immunology of acquired resistance to ticks (Brown, 1985) was worthwhile mentioning, together with a work on mucosa-associated immune system in rabbits (Befus and Bienenstock in Hay, 1982), a work on the functions of immunoglobulins of rodents (Binaghi, 1986), and finally a work on the complement system (Linscott, 1986). These two last topics were dealt with in several publications. As far as immunoglobulins were concerned, Mage et al. (1984) pointed out that immunoglobulin heavy chains in rabbits were strongly endowed with alternative forms which were genetically controlled and serologically identifiable.

The sequences of several genes coding for variable regions in heavy chains were known. Martens et al. (1984) tried to sequence genes encoding the gamma and epsilon constant regions. Knight et al. (1985) found 4 genes in the constant regions of alpha chains. Mc Cornack and al. (1985) described some interactions between genes in variable regions of heavy chains. Gallarda (1987) studied the organization in a zone of 600 kilobases containing about 100 genes encoding a variable region. The interval between gene was close to 6 kilobases. Lamoyi and Mage (1987) described a segment of 4.3 kilobases containing 3 genes encoding a variable region. These genes were sequenced and compared to homologous genes in mice and Man. Kelus and Weiss (1986) identified a mutation which undoubtedly affected a control element in the synthesis of variable regions. The breed manifesting this mutation was baptised "Alicia".

Similar works were carried out on lambda light chains (Hayzer et al., 1987). Polymorphisms of kappa light chains were described (Heidman and Rougeon, 1984; Hole et al., 1987). In a breed under mutation known as "Basilea", Mage et al. (1984) found a minor "K2 (bas)" light chain. The "bas" allele segregated as an allele or a pseudo-allele. It would appear to exist as a negative relation between litter size and the percentage of homozygous "bas" animals in each litter.

In conclusion of this section on immunogenetics it was considered worthwhile mentioning that in a Japanese breed of Angora rabbits the C-6 component in the complement was absent. This deficiency was transmitted by means of a recessive autosomal character. Always in Japan, Komatsu (1985) developed an hereditary deficiency with regard to total haemolytic complement activity (CH-50) by carrying out a diverging selection experiment on this criterion from which an heritability of 0.3 was estimated. By crossbreeding samples of the low strain he obtained offspring presenting deficiencies in certain components of the complement. Finally, genes of the major histocompatibility complex were described. Authors were interested either in class I genes (Tykocinski et al., 1985; Rebeire et al., 1987), or in class II genes (Le Guern et al., 1985 and 1987; Sittisonbut and Knight, 1986). On a much more practical perspective Sokolovskaka (1985) suggested to inject leukocytes into does from the father of the litter, hoping to reduce embryonic mortality.

#### D. Attempts to transfer genes in rabbits

As far as it was known, at least 5 teams had carried out some gene transfers in rabbits (Table 6). Hammer et al. (1985) as well as Brem et al. (1985 and 1986) built up a combination containing the promoter region of the mouse gene for MT (methallothionein) and the structural gene coding for the human growth hormone. This combination was then injected in the nucleus of an embryo at its unicellular stage.

About 10 % of eggs handled developed after being reimplanted and a 10 % to 20 % out of them had integrated the combination. As it happened with mice, the number of copies present in the genome of rabbits was very unstable, ranging from 1 to 490 for Hammer et al. (1985). Unfortunately the authors involved did not leave additional information on the translation of the transferred gene, on its phenotypic effects and on an eventual Mendelian transmission. Hammer et al. (1985) only indicated that the rabbit on which they observed a translation of the gene have a mandibular prognathism. Strojek (1986) made use of a combination including the uteroglobin gene and the chloramphenicol acetyltransferase (CH) bacterial gene. The implantation rate of eggs after being handled was about 30 %. 15 % of these gave birth to a new rabbit, 27 % of which (10 out of 37) were transgenic. Strojek pointed out that transferred genes showed structural alterations at times.

Deloui's and Houdebine's teams (Physiology Station, INRA - Jouy) attempted to carry out some gene transfers in rabbits (Houdebine, 1987), but their results had not been published.

The technique of transferring genes via micro-injection, first tested on mice, appeared to work even with rabbits. The operation's yield was low and there was very little data available with regard to expression and transmission of transferred genes. This technique still needed improving. It was possible that attempts would be made shortly employing a retrovirus as a vector. Besides improving the technique, transferring genes posed several questions.

First of all, the variability of translation modalities, the phenotypic effects and the modalities of Mendelian transmission observed with transgenic mice sufficiently highlighted present ignorance with regard to the working of genomes in superior animals. Secondly, which gene would be considered as suitable for transferring into rabbits? Experiments carried out on mice showed the advantages and disadvantages derived from the gene of the growth hormone. Although mice obtained in certain cases adult sizes which were double those of control animals, their mortality rate was high, there were problems with regard to their fertility and their character transmission was hazardous. Having said that, giant races were ready and available with rabbits and it did not appear worthwhile to create more of them.

All available knowledge on the genome present in rabbits was synthesized in previous chapters. Among the genes so far localized and sequenced none appeared excessively suitable to be considered for transferring with a view to an immediate zotechnic application. Some major genes highlighted in other species, such as the "culard" gene in pigs or the "Booroola" gene in sheep, held at least a scientific interest with regard to rabbits. How would they express themselves and what would be their effects in other species? But before considering such an experimentation, these genes were to be localized and sequenced. Once more, a true valorization of a transfer operation required a deeper knowledge of the genomes in species of domestic animals.

## II - STUDY AND COMPARISON OF RABBIT POPULATION, BREEDS AND STRAINS

Members of a domestic species were classified under the three categories of population, breed and strain. With regard to rabbits, a population was defined as a group reared with an homogeneous method of production within a region. Regional ecological characteristics and production methods together with breeders' interventions shaped a population genetic patrimony. French farm rabbits (Arnold and Chastang, 1983) and Baladi rabbits in Egypt were taken as good examples of populations. The next step in evolution was the breed where breeders' action was more important. Breeders would define a standard and select the animals that best complied to that standard. Many selection criteria could be adopted: physical format and structure, coat coloration and characteristics, etc... In Europe and North America breeds were enthusiastically selected mainly by fancy breeders (Steichen, 1986 a and b). The degree of influence derived from regional ecological characteristics and production methods would not be as significant with breeds as with populations. Breeds resulted to be more genetically homogeneous than populations. Selection practices aiming at achieving the highest degree of conformity with chosen standards led to excesses. Breeders were exclusively interested in visible phenotypic features while neglecting production characters. They carried out mating between closely related samples. A strain was made up of a few rabbits obtained from one or several populations or breeds. A strain was singled out by means of a selection having as object a rather limited number of criteria. Such a selection assured a more homogeneous level of performance (litter size, growth rate, etc...) within a strain than there would be in a breed. The size of a strain was much smaller than that of a breed (at most a few dozen bucks and a few hundred does). The introduction of rabbits from a different strain was rare.

35 publications of our sample dealt with the analysis of a population, breed or strain. These monographs were certainly interesting, but the results presented did not appear easily exploitable, since litter size or growth rate could not be regarded as significant in absolute terms. They were closely related to the breeding conditions (feed, habitat, reproduction rhythm, etc...) in which rabbits were reared. 69 other publications compared rabbit populations, breeds or strain with one another, but the authors often forgot to outline breeding conditions and to define the origins of their rabbits. In some instances of crossbreeding, experimental procedures were so often incomplete that they prevented the carrying out of a full genetic interpretation.

Before tackling the study reports in themselves, it was thought useful to present the inventories drawn by certain countries with regard to their rabbit populations. To conclude, a perspective on the steps taken with regard to conservation will be considered.

### A. Some inventories.

At the time of the Rome Conference (Poujardieu, 1984) 4 recommendations were adopted out of the round table discussion on genetic improvements, aiming at employing the better adapted breeds while maintaining a reasonable degree of genetic variability. The following actions seemed necessary:

1. identification and compilation of breeds inventories;
2. careful description of phenotypic characteristics, reproduction and production in every breed;
3. assessment of locally adapted breeds in different countries;
4. acquisition of information on the behaviour of different breeds.

A questionnaire was designed to carry out these actions and the FAO translated it in English and Chinese. Unfortunately, the World Rabbit Science Association was not able to find enough funds for its propagation. This difficulty will possibly be overcome in occasion of the Budapest Conference.

Inventories on a national scale have already been compiled. The French Ministry of Agriculture carried out an investigation in 1982 among rabbit breeding farms (Table 17). Investigators singled out 2 types of samples: in one were the totality of breeders, in the other only breeders belonging to a producers' association. In both cases pure bred does represented a percentage of between 20 % and 25 % of the total. "Hybrid" does, which were the result of a commercial network for the spreading of genetic progress, represented 25 % of total rabbits and 58 % of total rabbits reared by breeders belonging to an association. The difference was born by other types of "hybrids": a badly defined category of does undoubtedly originating from self-renewal as well as various crossbreeding operations. The situation had evolved considerably since 1982, but this type of investigation remained very interesting.

Another easy to use source of information consisted of catalogues of exhibitions. Rudolph (1986) made use of them to draw an inventory of rabbit races in his country. Less complete, but not the least any lesser interesting descriptions were carried out by Marchant (1987) in Great Britain, Niedzwiadek (1982) in Poland, Palkin (1987) in the Soviet Union. Cheeke (1983) outlined the situation of local rabbit races in Indonesia. The New Zealand White and Californian races seemed to impose themselves everywhere on local breeds.

#### B. Breed monographs

The contents of a study, or monograph, carried out on a breed can be very wide ranging. The aim was to outline the 4 points mentioned earlier. This objective was achieved by the Zaragoza's team with the Spanish Common breed (Zaragoza et al., 1985 and 1987). They assigned a place to this breed in a historical perspective before defining its standard. They subsequently studied its zootechnic potential and worked out a series of genetic distances in relation to other breeds making use of biochemical polymorphisms. A similar step was taken in France for the French Silver breed (Perrier and Chevalier, 1984; Perrier et al., 1986) and the Bourbonnais Grey breed (Pilandon et al. 1986). The 2 breeds zootechnic potential was determined by comparison with "hybrid" does suited to the breeding practices in use (metal cages, intensive reproduction rhythm, etc...). Different breeding conditions (cement hutches, extensive reproduction rhythm, etc...) could have given different results. A rather extensive evaluation of their carcass quality was carried out. Other studies of this kind were being performed in Italy (Grey rabbit - Toscano et al., 1983; Zoccarto et al., 1985), in Spain (Spanish Giant - Sierra Alfranca and Lopez Sanchez, 1984; Lopez Sanchez and Sierra Alfranca, 1986) and in Poland (Large Steel Gray Ram - Holitscher, 1986).

Among other monographs mention needs to be made of Niedzwiadek et al. (1983) for the Termonde White race, and Miroshnichenko (1984), for the Soviet Chincilla race. The latter breed, bred for both its meat and fur, showed good litter size and weight. Selection was performed according to its coat density. Sartika and Diwyanto (1985) described a local rabbit population in Indonesia. Does were of medium size (2 to 2.5 Kg) and reared 5.5 offspring with an average weight of 460g each at weaning. Some authors also studied "hybrid" does which were the outcome of commercial schemes. Battaglini et al. (1984) studied the productive life of 978 Hyla does in an Italian breeding farm. The life span of these does was on average 515 days. They gave birth to 7.84 litters a year and reared 48.7 offspring a year. This was a remarkable study in so far as it was not limited to average figures obtained on the first 3 litters, but it analysed does' productive life as a whole. It was the closely concerned with breeders' preoccupations. A singular factor in this breeding farm was the very low elimination rate observed, compared with the rates usually found (28 % of does eliminated by the end of the first year; 87 % by the end of the second year).

Several publications dealt with Hyplus does. On a sample of more than 60 000 litters in 70 breeding farms run by a technic-economic managing board. Litter sizes were respectively 9.30 at birth, 8.15 at weaning and 7.14 when sold (Anonymous, 1988). This sample was not representative of average rabbit breeding in France. These results only indicated the "hybrid" does' production potential in well run farms. The growth of rabbits born from these does (Jouve et al., 1986) as well as that of the strain from which the breeding males performing the final cross descended (Retailleu and Baumier, 1986) were also studied.



An advantage in working with domestic rabbits was that problems of genetic variability could be solved by turning to wild rabbits ("lapins de Garenne") belonging to the same species. Arana and Zaragoza (1987) described the genetic abundance of several wild rabbit populations. These populations were isolated genetically islands. Nath and Rao (1985 a and b) compared the growth and carcass of these 2 kinds of rabbits. Wild rabbits were lighter. At slaughtering they had a lower yield, thinner and less resistance skin, and their meat possessed a higher Ph and water retention capacity. While West European domestic rabbits were taken to descend from previously wild population ("lapin de garenne"), the origins of Chinese domestic rabbits was still argued upon. According to some authors (Chen, 1984) they were tamed by the Chinese themselves about 2000 years ago, but others (Luo, 1983) suggested that they did not exist in ancient China. For the latter, rabbits were introduced at a later period by silk traders. This hypothesis was supported by the specific diffusion area of the *Oryctolagus cuniculus*.

### C. Comparison of populations and breeds

Table 18 shows the populations studied by different authors. In relation to the existing number of rabbit populations and strains, the number studied was small. This appeared particularly true with regard to local rabbit populations which had only too seldom been taken into consideration. But there were nonetheless a few exceptions (Matheron and Dolet, 1986; Rahumathulla et al., 1986; Kosba et al., 1985). Many authors studied the New Zealand White and Californian breeds, but have these 2 breeds real predominance in all countries? In the hypothesis that each of these 2 breeds being homogeneous, one of them could serve as a point of reference; but is this hypothesis truly feasible? Although the number of medium-sized breeds studied appeared relatively high, in reality it was hardly superior to the number of giant races studied. Very few studies were carried out on small format breeds. Brun and Rouvier (1984 and 1986) carried forward a study of genetic effects on features of litters descending from several breeds. They assessed direct, maternal and grandmaternal genetic effects, direct and maternal heterosis among the 1077 (New Zealand White), 1066 (Californian) and 1088 (Small Russian) strains with reference to a crossbreeding experiment carried out in 1971 and 1972. They carried forward their analysis by assessing once more the same effects with reference to a crossbreeding experiment carried out in 1979 and 1980 between the 1077 and 1066 stains.

Table 19 shows a few results with regard to litter sizes. Litters from the New Zealand White were almost always reported to be superior in size to those of the Californian breed.

These results within the New Zealand White breed itself appeared very unstable, denoting an important degree of variability in breeding conditions. This breed was undoubtedly made up of a wide range of populations, being present world wide, which did not have much in common except for the albino character. Litters produced by "hybrid" does were superior in size than those obtained from New Zealand White does. Heterosis effects were not worked out often enough. Direct heterosis on litter size varied between 10 % and 15 %, except for Lahiri and Mahajan's experiments where it was negative. In tropical countries (India, Egypt), the litter size of giant breeds (Grey Giant, White Flemish Giant, White Giant etc..) was equal to or superior to that of medium-sized races (Affifi and Emara, 1987; Damodar and Jakta, 1985; Cahiri and Mahajan, 1983 and 1984). There were other breeds the potential of which, compared to medium-sized ones, appeared significantly interesting within the parameters of their breeding environment: the Soviet Chinchilla (Gugushvili, 1981; Lahiri and Mahajan, 1983 and 1984), the French Silver which produced litter sizes comparable to those of a hybrid doe (Perrier and Chevalier, 1984) and the Sandy race (Rahumathulla et al., 1986). With regard to the interest given for local rabbit populations, Matheron and Dolet's results (1986) deserved a mention. They have compared does descending from various crossbreeding operations with local "Creole" does and New Zealand White does, in tropical commercial breeding farms. The number of live born rabbits were respectively 6.72/6.21/6.71 at birth and 4.54/4.42/5.14 at weaning. Local "Creole" does made up at weaning for their initial lower reproduction rates compared to does descending from crossbreeding attempts. The New Zealand White proved to possess a high degree of adaptation. The results obtained supported the need of setting up a policy of genetic improvements to avoid poorly matched crossbreeding by taking into account certain quality features in local populations.

Table 20 shows results relating to growth and carcass composition. A wider range of results was permitted following the consultation of Masoero's synthesis (1982) whose table presentation was adopted. The results of Table 20 confirmed giant races' high growth rate and a less important rate of precocity (Auxilia and Masoero, 1986; Lukefahr et al., 1984). The French Silver usually stood out for its

good growth rate among medium-sized race (Auxilia and Masoero, 1986 ; Desalvo and Zucchi, 1984 ; Masoero et al., 1985 ; Perrier et al., 1986). This was equally true from time to time for the Vienna Blue (Desalvo and Zucchi, 1984 ; Masoero et al., 1985). The Bourbonnais Grey, a rather small-sized, provided a better yield at slaughter than one born from a hybrid doe. Hybrid offspring often reported a superior growth rate than the New Zealand White. Jakubec et al., (1985 a and b 1986) studied the genetic weight components at 84 days basing it on 2 highly inbred lines and their crosses. The authors made use of a model with direct additive effect, direct dominance effect, and grandmaternal additive effect. Most effects were not significative because the number of animals involved was too restricted.

Only a few authors showed any interest in the fur of these animals. Rochambeau and Vrillon (1985) carried out comparisons between the fur obtained from rabbits which did not undergo any mutation and Rex rabbits. Furs tended to differ quite a lot from one another. To have any chance to obtain a good quality fur, it was necessary to delay slaughtering. By changing from a summer nycthemeral rhythm (16 hours a day) to a winter one (8 hours a day) when the animals were 9 weeks old, their 3rd coat was fully grown by the age of 17 weeks, 8 weeks later. By then, furs had achieved a good standard (Vrillon et al., 1988). Tineaev (1984) compared Chinchilla and Californian rabbits and he reported that although the former breed was heavier, the density of its fur was not as good as the latter one. At the end of May, a lower percentage of Chincillias has finished shedding.

To conclude this revision of comparisons carried out between breeds, it was felt necessary to mention the works of several authors on sperm characteristics (Amin et al., 1983 ; Dubiel et al., 1985 ; El-Ezz et al., 1985 ; Miros et al., 1989). They studied the variations of classic parameters (quantity ejaculated, motility, percentage of abnormal spermatozoons, etc) in relation to the buck race and other variation factors such as season. Differences were undoubtedly identified between breeds, but they were not highly exploitable since the authors did not link them with "in vivo" fertility differences.

#### D. Conservation programmes

Conservation of genetic resources in species of domestic animals aroused great enthusiasm some years ago. A national data bank for farmyard animals was created in France (Arnold and Rochambeau, 1983). This movement permitted the study of various local breeds or populations, as it will be seen, and to take an interest in their history (Data Bank (CONSERVATOIRE), 1981). This movement lost its initial importance, at least in France. But the problem continued to persist since available inventories and studies carried out remained fragmentary in nature. Some populations and breeds have already or are going to disappear and, as Lukefahr (1988) pointed out, popular breeds as the New Zealand White took over the place of local populations even before they were evaluated. Lukefahr (1988) proposed to standardize the criteria by which races were studied and to set up a data bank.

Nowadays a number of ideas have originated from all the reflexion entertained on the theme of conservation :

1. Why conserve ? What to conserve ? These questions remained unanswered. Conservation was supposed to require the existence of an instantaneous consensus that must not be questioned. To conserve a maximum degree of genetic variability within a species would be an insurance and a wager for the future. But does genetic variability as it is measured nowadays correspond to reality ? Is it truly certain that there are no other potential reserves of genetic variability in the inexpressed portion of the genome or in mechanisms still unknown ?
2. Man's influence on the evolution of domestic animals has been predominant. It was regarded as undesirable to discontinue this association animal/breeding - method/man.
3. To conserve populations, financing on regional, national and/or international levels was regarded as necessary. Light but efficient organisation to co-ordinate actions and to centralize information was regarded as indispensable at the various levels.
4. Any project bringing together breeders and rabbits towards a well defined objective should be considered as interesting. The conservation of a certain degree of variability among breeders and breeding methods was regarded as a prerequisite to conserve genetic variability.

### III - MECANISMS

This section includes a study of subagent physiological mechanisms, genetic promoters and selection experiments.

#### A. Mechanisms influencing litter size

The works of the Toulouse and Tours teams in France and the Valencia team in Spain supplied further information on the biological components of litter size. The other component of fecundity, fertility, was strangely not studied at length.

##### 1. Ovulation rate

Hulot and Mariana (1985) and Mariana and Hulot (1986) carried forward a comparative study on breeds 1077 and 1066, selected at Toulouse in experimental conditions. The strain 1066 showed to be advantaged by 2 ovules compared with strain 1077. To give this difference an explanation these authors studied preovulatory follicles and their growth. The does of strain 1066 presented a bigger number of healthy preovulatory follicles. There were no differences with regard to average size or surface, size distribution or atresy rate in the follicles. But growth rate resulted to be higher in strain 1077. All that did not nevertheless explain the differences in ovulation rates and researches were directed towards studying differences in the rate of gonadotropic hormones receptivity. To complete, the availability of several works on ovulation induction deserved mentioning (Hulot and Mariana, 1986 ; Fan et al., 1986 ; Molina et al., 1987).

##### 2. Embryonic viability

The number of implantation sites or the number of live embryos at a given age increased with ovulation rate. The relation was generally curvilinear (Pla et al., 1985 ; Molina et al., 1986 ; Bolet et al., 1988). Having said that Bolet et al. (1988) showed that in certain strains the notion of an ideal ovulation rate did not exist. The relation appeared no longer curvilinear and embryonic viability seemed to remain constant irrespective of ovulation rates. The effects derived from different ovulation rates on embryonic viability decreased as gestation progressed (MOLINA et al. 1987).

With a wider perspective, Pla et al. (1983) tried to locate the influence of embryo numbers on embryonic viability taking into account other factors (embryo dimensions, weight of placentas, live weight of does, etc.).

The Toulouse team in collaboration with Jouy and his team extended the comparison of strains 1066 and 1077 to their embryonic viability (Torres et al., 1986 and 1987 a and b ; Bolet and Theau-Clément, 1988). Strain 1077 was endowed with a better viability, which was partly due to maternal uterine effects and direct embryo effects. Strain 1077 blastocysts were bigger. According to Molina et al. (1987), that did not explain the differences in pre-implantation mortality rates within the strains. But it was possible to come to different conclusions when different strains were compared. Bolet and Theau-Clément (1988) observed a very precocious embryonic mortality in strain 1066. Was it the result of the ovules not having been fertilized or a lower segmentation speed ?

##### 3. Influence of consanguinity

Kliment and Jamriska (1985) measured the differences in litter size of does the inbreeding coefficient of which varied between 0 and 0.785. A 1 % increase in the rate of inbreeding corresponded to a 0.039 decrease in litter size ; that is, the equivalent of a 0,5 % decrease in the size of litters of unrelated animals. These results were in coherence with others obtained in previous studies.

Zelnic (1984) measured the effects of inbreeding coefficients on the weight of individual rabbits. Their inbreeding coefficients varied between 0 and 0.67. A 1 % increase corresponded to a 0.24 % fall in weight at birth, 0.38 % at 8 weeks and 0.11 % at 24 weeks in relation to the weight of unrelated animals.

#### 4. Influence of number of nipples

The number of nipples constituted a measurable component of maternal and grandmaternal effects. According to Szendro and Kampits (1985), a bigger number of nipples appeared to be accompanied by an increase in the litter size of live born rabbits found at birth and at weaning. The results Rochambeau et al. (1988) obtained were different. These authors established a connection between ovulation rate and total number of nipples across different breeds. Besides, Lukefahr et al. (1984) observed a direct heterosis effect influencing the number of nipples. At the same time no connection was reported with litter size. It was simply possible to establish a general tendency for litter size at weaning. Taking up an idea first presented by Fleishhauer et al. (1985), it was observed that this tendency became significant when there was a larger number of live born rabbits than nipples. Taking such a criterion into consideration with regard to very prolific breeds could give interesting results.

#### B. Meat production

Ouhayoun (1983 and 1984) synthesized available knowledge on growth and development of domestic rabbits. There existed a strong genetic variability between and within races. Adult live weight largely determined growth rate and precocity as well as body composition. He also analysed the influence derived from environmental factors. Ouhayoun et al. (1987) analysed feeding factors in an other synthesis. These 3 publications completed nicely Masoero's work (1982).

Researchers in the Toulouse team studied possible interactions between genotype and feed protein levels (Ouhayoun and Cheriet 1983 ; Ouhayoun and Delmas, 1983). These two factors proved to have additive effects. In a comparison carried out between rabbits from a local population and offspring from a particular strain being selected for its high growth rate, the latters achieved a considerably higher final growth (+ 3 %). They also proved to be more efficient in processing feed (Gross Feed Efficiency : 6 %). Their carcass presented less fat (- 9 %) while showing more muscle tissue (+ 12 %) and less bone (- 8 %).

Other researchers within this group (Poujardieu et al., 1986 ; Ouhayoun et al., 1986) studied how to produce heavy carcasses (1,8 - 2 kg versus the usual 1.2 - 1.4 kg) from medium-sized breeds. The carcasses of animals fed *ad lib.* and slaughtered at 15 weeks old achieved a weight of 1.8 kg. This appeared to be the best of the solutions considered. Carcass costing per kg. increased by 22 % compared with animals slaughtered at 11 weeks. Yield was improved (+ 9 %) but carcasses presented a higher rate of fat. It was realised that such a delayed slaughtering enabled to gather better quality furs (Rochambeau and Vrillon, 1985). Taylor and Johnston (1984) nevertheless demonstrated that to obtain maximum quantity of first quality skin on Rex rabbits, it was advisable to ration feed down to 75 % of the original '*ad libitum*' supply.

Purchase of rabbit feed constituted the main source of expenditure for breeders making use of granulated feed. Gross feed efficiency was then regarded as an important selection criterion. Unfortunately gross feed efficiency was expensive to estimate and difficult to interpret, that explained why it was often neglected by experimenters. Masoero (1982) established that the link between growth rate and gross feed efficiency was not sufficiently clear for an efficient indirect selection policy to be worked out. This resulted especially true for fixed age tests (for example, 28-77 days). To make a better use of this connection Masoero (1982) advised to work on age/weight tests (28 days up to 2,4 kg) or to carry on control till a later age.

To achieve a closer analysis of gross feed efficiency Masoero et al. (1985) worked out the consumption rate maintaining constant weight (weight at the beginning and end of the experiment) as well as residual gross feed efficiency on a constant growth rate. Brun and Ouhayoun (1988) proceeded on similar lines.

#### C. Genetic parameters

Khalil et al. (1986) compiled a bibliographical synthesis of phenotypic and genetic parameters determining the characters for meat production in rabbits. Although this bibliography was strangely incomplete, it provided a general view of genetic parameters in rabbits. The estimations put together by

Khalil et al. (1986) are presented in Table 21 in the form of a diagram. Most times estimations of litter size heritability were included between 0 and 0.4. The estimated distribution median did not appear clear. Estimations of the heritability of litter total weight varied during the same period within a median of between 0.10 and 0.20. Estimations of the heritability in individual body weight tended to increase with age. The median was below 0.20 in individual body weight at weaning and above 0.45 for data recorded after weaning.

Moreover, Khalil's synthesis (1986) confirmed the phenotypic and genetic correlations between these characters. Litter sizes at different ages were correlated with one another as well as with total litter weight. Individual body weight at different ages presented a positive correlation with each other and a negative one with litter size. Masoero's synthesis (1982) remained the main reference with regard to connections between growth rate and gross feed efficiency.

Table 22 presents a few estimations on heritability published after Khalil's et al. synthesis (1986). The very high values estimated by Patras (1985) on the heritability of nipple number (0,89) clearly stood out.

#### D. Selection experiments

Until the last world conference on rabbit breeding (Rome, 1984) results of selection experiments on rabbit performance were few. Since that year, the results of 5 experiments have been published. Selection experiments provided good biological material to study the mechanisms controlling zootechnic characters. Selection experiments were especially useful to carry out studies on genetic connections between characters. New strains born out of selection experiments were eventually to be found in farm breeding. At the same time, productivity in its various forms must not be neglected. Firstly, selection experiments dealing with litter size will be analysed, then those dealing with growth rate, and finally, mention will be made of other experiments going on or planned to take place.

##### 1. Selection experiments on litter size

Table 23 presents a synthesis of the 4 series of results available at the moment. The oldest experiment was started in Toulouse in 1976 (Matheron and Poujardieu, 1984). A team in Valencia (Estany et al., 1988) carried forward a simultaneous selection on 4 strains, two of which were concerned with litter size at weaning. A selection experiment took place in Tanzania (Mgheni and Christensen, 1985) and another in India (Narayaw et al., 1985).

The selection criterion was always litter at weaning, except for Narayan et al. (1985) who decided for litter size at 14 days after birth. Three strains were selected according to both their own performance and that of related samples whilst two others were selected according only to their own performance. The selection was performed on populations of more or less the same size (20 to 30 bucks and 120 does); except for Mgheni and Christensen (1985), but their experiment only covered 4 generations. Three other experiments covered 6 to 8 generations, but selection with strain V in Valencia had only been happening for one generation. Data were worked out in relation to a control breed, except for Valencia where estimations were calculated by a BLUP. Moreover, Mgheni and Christensen (1985) also operated on high and low strains. The levels of direct response varied between - 0.05 and + 0.35 offspring per litter and per generation. Mgheni and Christensen observed a - 0.43 response in their low strain. Estimations carried out on the realized heritability were between 0 and 0.30. Direct response was low and varied from one experiment to another. New estimations based on the experiments taking place in Valencia and Toulouse will perhaps provide less ambiguous results in future. Various causes (low selection intensity, antagonistic effects in opposition to direct and maternal effects, etc.) were put forward by the authors in an attempt to find an explanation for observed responses being lower than expected.

The correlated response on litter sizes at birth was higher than direct response in one experiment (Matheron and Poujardieu, 1984). It was similar to the level of direct response in another experiment in which correlated response was studied (Estany et al., 1988). The level of correlated response on individual live weight at weaning varied from one experiment to another: positive for Estany's

strain (1988), close to 0 for Matheron's and Poujardieu's strain 1077 (1984), negative for Estany's et al. First generation of strain V (1984). Other correlated responses were studied by the Toulouse team. Their selected strain (1077) presented a larger number of nipples (9.08 versus 8.86) compared with the control strain (9077) (Rochambeau et al., 1988). The strain undergoing selection achieved a higher rate of ovulation (11.4 versus 10.4). It also had a higher number of implantation sites and live embryos at 14 days (9.7 versus 9.2 and 9.2 and 8.8 versus 7.9 respectively) (Bolet et al., 1988). The doe adult body weight of the strain under-going selection was 10 % less than that of the control strain (Brun and Ouhayoun, 1988). A comparative study of strains 1077 and 9077 had not long been started and it was expected to provide more elements on response modalities.

## 2. Selection experiments on growth rate after weaning

The results of 3 experiments were available. The first one had already been partially analysed by Rouvier et al. (1980) in occasion of the Barcelona Conference (Fuente et al., 1986). The second one took place in Tanzania (Mgheni and Christensen, 1985). The third one dealt with one of the strains reared in Valencia (Estany et al., 1987). Although all authors appeared to agree for a selection based on the performance individual, their selection criteria were slightly different : daily growth rate in Toulouse (between 28 and 77 days), individual live weight at 112 days in Morogoro, weight increase between weaning and 77 days in Valencia. Their populations were smaller than previously (12 to 20 bucks ; 40 to 80 does). The direct responses observed were respectively of + 0.83 g, + 52 g, + 33 g. Mgheni and Christensen (1985) had observed a response of - 75 g in their low strain. The realized heritability had been estimated between 0.11 and 0.31. These direct responses were coupled with a correlated response on weight at 10 or 11 weeks and weight maintenance at weaning. These responses represented 1 % to 2 % of the selected character average. Selection based on growth rate after weaning appeared efficient with rabbits. Nevertheless the level of observed responses was lower than expected. In an attempt to explain this difference the authors put forward possible antagonism between direct and maternal effects, low selection intensity, etc.

There were no available data on gross feed efficiency for these strains. The correlated response on litter size was positive in Estany's et al. experiment (1987) and negative in Fuente's et al. (1986). To give this divergence in results an explanation, Estany et al. (1987) pointed out that strain B had suffered health problems. An analysis of selection differentials on litter size of selected strains in Toulouse would explain this negative correlated response (results not yet published). Besides, both authors observed a fall in fitness in the strains selected for its growth rate after weaning. The data published by Torres et al. (1986 and 1987) showed that there was a larger percentage of does which never managed to rear a litter of their own in strain B than strain A, the strain selected according to litter size at weaning. Elimination rate within does of strain B was higher than within strain A. Fuente et al. (1986) reported similar observations. As Masoero (1982) remarked, the degree of fertility, prolificacy, and longevity of strains selected for their growth rate after weaning must not be neglected.

## 3. Other selection experiments being carried out or planned

Huang (1987) performed a diverging selection experiment on growth rate and gross feed efficiency. Komatsu (1985) based its selection criterion on total haemolytic activity of the complement, whilst Miroschnichenko (1984) chose coat density as his criterion. The results of these experiments did not appear to be available.

In the occasion of the Budapest conference, 2 new selection experiments were presented in a joint Franco-Spanish project. These experiments were performed on overlapping generations. The Spanish team from Barcelona selected the does that bore litters with the highest total live weight, to start with ; in their following stage they kept the offspring reporting the highest growth rate after weaning (Valls et al., 1985, Rafael et al., 1988). The French team from Toulouse carried out their selection according to live weight at weaning per doe and per year (Rochambeau et al. 1988).

The amount of data resulting from selection experiments on rabbits was expected to keep increasing.

#### E. Elements determining the productive life of does

Rabbits are bred essentially for their meat. The majority of rabbit meat in Western Europe is produced to be sold on the open market. Therefore profit is obviously tied to litter size and growth rate of the breeds reared. Revenue also depends on the productive elements of the life of does; that is, their age at their first litter, number of litters a doe provides before its elimination, etc.. The elements determining the productive life of does are the result of a combination of genetic and non-genetic factors. The effects of some of these factors will be analysed making reference to different publications that became available in the last few years. The analysis shall give preference to genetic factors.

There are instances in certain countries where rabbits are bred with a different aim in mind: fur production, meat production for personal consumption, etc.. While still holding a certain amount of interest, in this case the analysis of a doe's productive life needs to be viewed from a different perspective.

On one hand, a doe's productive life was taken to indicate the interval of time between its birth and its elimination (natural or induced death); that is, its longevity. Some authors made productive life begin with a doe's first mating. On the other hand, a doe's productive life was also taken to indicate a doe's production within that period. The production was often broken down to small units. This production was tied to several elements: age of reproductive maturity, age of elimination, fertility, prolificacy, litter weight. Fertility was defined as the percentage of does actually littering in relation to total number of does being served. It was often estimated by working out the interval of time between the birth of 2 successive litters. Estimations of this element were rather global in nature since they depended on doe aptitude to be fertilized and on doe aptitude to follow the reproduction rhythm imposed by breeders. Prolificacy was the number of offspring making up a litter, measured at birth and

product of fertility via prolificacy, was defined as the number of offspring per doe being served. Finally, total litter weight was a function of litter size and individual offspring weight.

These elements in a doe's productive life were tied with each other and interacted as a result of the breeding method applied. So, in a breeding farm reporting a high post-weaning mortality rate, Morisse (1986 and 1987 a and b) constituted "a posteriori" 3 litter samples in function of their viability between birth and sale. Morisse singled out litters with a viability rate above 85 %, included between 65 % and 85 %, and below 65 %. The total number of offspring in the first sample was of 8,4 at birth and 7,6 at slaughtering. The litter total weight at slaughtering was of 16,9 kg. If for each of these variables the index of 100 was attributed to litters with a high rate of viability, the other 2 groups would show the following values. Total number of offspring at birth: 113 and 115; number of live offspring at slaughtering: 89 and 58; total litter weight at slaughtering: 89 and 59. It did not seem possible to generalize the results of this study and therefore conclude, as its author did, that there existed a connection between prolificacy and mortality rate before slaughtering. It was nevertheless a reminder that there existed a close connection between litter size at birth and at slaughtering only while dealing with averages. Moreover, was not prolificacy only be enhanced when breeding conditions permitted it?

From a more general point of view, as litter size at birth increased, the total rate of offspring viability fell but litter size at weaning and slaughtering presented an overall increase. This conclusion was reached following a critical analysis of the observations present in the bibliography. There appeared to exist a minimum weight at birth and at weaning below which survival probabilities were very low. Torres et al. (1986) studied the frequency of occurrence of these 'puny' offspring at birth as a function of litter size. The average number of puny offspring was of 0.05 in litters of 6, 0.27 in litters of 10 and 0.64 in litters of 14. In a different study, Torres et al. (1986) showed that at constant litter size, the more prolific breeds bore the heaviest offspring at birth. They did not report different post-weaning mortality rates in breeds with differing levels of prolificacy. Besides, Torres et al. (1986) had established that live rabbits at slaughtering were on average heavier at weaning by about 30 g (6 % average weight) than offspring dying at an earlier phase of the fattening up period. These observations confirmed that even if viability decreased in a negative relation to prolificacy, it appeared interesting to increase prolificacy through selection, if breeding conditions were to allow it.

1) Comparison of elements determining the productive life of does from several genotypes

Coudert et al. (1984) and Coudert and Brun (1986) compared the productive lives of does descending from strains 1077 and 1066, and does born out of crossbreeding experiments between these 2 strains. They observed significant differences between the resulting strains. Strain 1077 reported a better longevity than strain 1066. Instances of elimination in strain 1077 were mainly due to mortality. Does from strain 1066 were not as sound healthwise. Instances of elimination were mainly the result of induced death. Whole litters disappeared between birth and weaning in strain 1066. Crossbred does reported an intermediate rate of viability. It was unusual to find no heterosis in this "adaptation" character.

Torres et al. (1986 and 1987) compared different elements in the productive life of does from strains selected in Valencia. They also reported differences between their 4 strains with regard to longevity or causes for elimination. Strains selected for their litter size reported a better longevity than strains selected for their growth rate. Synthetic strains of recent creation reported a better longevity than older strains. Henriksen (1982) observed a higher mortality rate in a Rex strain than in a Danish Landrace strain bred in identical conditions.

2) Other variables in the elements determining productive life

The analysis shall be limited to the factors being potentially interactive with the genotype. Lebas and Coudert (1986) studied the effect of the age at which sexual initiation took place (15 to 20 weeks) on the elements in the productive life of does from strains 1077 and 1066. They concluded that the age at which sexual initiation took place had no effect on the elements the expression of which took place at a later period. Strain 1077 was more precocious than strain 1066; its fertility rate at 15 weeks was higher.

Grobner et al. (1985) arranged for does of different formats to be reared on diets which were more or less rich in calories and proteins. Due to the small size of the sample the results could not be taken as fully representative. These results constituted however an interesting working hypothesis. As the format of rabbits increased, their ingestion capacity increased more than proportionally which would enable them to take better advantage from feeding being low in calories and proteins. Ceruera et al. (1987 a and b) and Martinez et al. (1987) varied either the nourishing value of the diet or the rhythm of reproduction. These 2 factors altered the weight of does and it would be interesting to compare several genotypes in equivalent conditions.

Brun and Poujardieu (1986) tackled the problem from a different perspective. They looked for criteria which would outline the productive lives of 223 does from 4 different genotypes. They discriminated between litters from unipara does which were to be eliminated; litters which preceded any elimination and other litters of different parity. The more distinguishing characters were does live weight during palpation and does live weight fluctuations at the start of reproduction cycles. However, none of the criteria considered permitted to predict the length of their productive lives.

The productive lives of does progress as a rule within a series of aggressions. Breeders are responsible for the majority of these aggressions by forcing does to follow intensive rhythms of reproduction, by keeping them in poorly ventilated sites, by overruling social and reproductive behaviour traits, etc... Vastrade (1985 and 1986) described these behavioural traits and outlined their complexity. What happened when breeders' practices clashed with these behavioural traits? It has already been illustrated that there existed differences between genotypes with regard to their rate of adaptation to particular breeding environments. In collaboration with Coudert, Poujardieu studied the resistance rate of a strain to non-specific aggressions. An aggression was modelled by employing coccidia to attack precociously at each generation part of the animals forming the sample. The consequences of this aggression were assessed all along the does productive life. This procedure was repeated during 3 consecutive generations. Contrary to what previous data suggested (Coudert and Lebas, 1984), preliminary analyses of the new data obtained from this experiment indicated that does surviving the coccidia aggression were as productive as does not undergoing the aggression (Poujardieu and Coudert, unpublished results), although the weight of the former group was inferior to that of the latter one. The aggression did not prejudice the expression of a good rate of productivity. It did not however enable them to disclose the resistance level to non-specific aggressions.



The association of productivity and longevity within the same animal has been the aim of many rabbit breeders. To study the mechanisms permitting such an association, the TOULOUSE team (Rochambeau, 1985) created a strain from 16 "hyperfecund" does selected from French commercial breeding farms. An "hyperfecund" doe was defined as a doe having reared up to weaning, a significantly higher number of offspring per time unit during its productive life than other does in the same farm did. Selected "hyperfecund" does had terminated between 6 and 25 litters. In a farm where does had reared up to weaning an average of 25 offspring in 6 months (length time elapsing between the first and last weaning), an "hyperfecund" doe would report an average of 50 offspring for the same period. The farms at which the "hyperfecund" does were selected kept their own performance records. The strain had already been closed and the homogenisation and study phases were to start.

#### IV. METHODS FOR OBTAINING AND PROMOTING GENETIC IMPROVEMENTS

This theme was dealt with by 56 publications. Most of them were concerned with the applied aspects for obtaining and promoting genetic improvements. Nearly two thirds of the publications in the sample came from Spain, Italy or France. This sample gave prominence to a specific production area. The present synthesis is also concerned with this area of rational breeding.

##### A. Methods of obtaining genetic improvements

###### 1) Theoretical aspects

Geneticists in applied genetics working on rabbit selection make full use of all the means quantitative genetics provides them with. It was not possible to present a full synthesis of the achievements in quantitative genetics for the last 4 years, so that only a few publications dealing strictly with rabbit breeding were considered.

The Valencia team (Estany, 1987 ; Estany et al., 1988) analysed the advantages derived from the utilization of a B.L.U.P. (Best Linear Unbiased Predictor) to determine rabbit selections. With regard to the indices using the performances of related animals as they were made use of in TOULOUSE and VALENCIA, the BLUP also took into consideration the whole range of relations, particularly the relations on the male side, which could nevertheless be equally accounted for with classical indices. The complexity of the calculations resulting from the utilisation of the BLUP in related populations often led authors to neglect inbreeding. The BLUP also permitted to perform analyses of selection experiments (Sorensen and Kennedy, 1986 ; Estany, 1987 ; Estany et al., 1987 and 1988), but there was the need for a prior estimation of the rate of heritability of the selected character to be available (Thompson, 1986). The BLUP was particularly useful to assess indirect responses and study the connections between different characters. Starting off with a series of genetic parameters on 2 Egyptian populations, Khalil et al. (1987) worked out several indices to improve doe performance before weaning or individual live weight at 6, 8 and 12 weeks. Instead, Campo (1984) used the genetic parameters his bibliography provided him with and he set up a model for the selection of 2 strains. The first one was selected according to its post-weaning growth rate and litter size at weaning. This strain was to provide a terminal cross buck. The second one was selected, with a multiplicative index, according to litter size at weaning and individual live weight at weaning. This strain was to provide a terminal cross doe.

This terminal cross doe, improperly called "hybrid", was produced by the crossbreeding of a buck from one strain and a doe from another strain. This doe performance was the result of a combination of direct and indirect genetic effects and environmental factors. This doe being crossbred, direct effects as well as maternal effects presented heterosis effects. The simplest strategy to adopt to improve this doe's performance would consist of choosing strains between which there existed heterosis effects and so select these strains for their eventual complementary characters. That was the strategy employed in Toulouse to obtain the crossbred doe 1067, the point of departure being a buck of strain 1066 selected according to litter size at birth and a doe of strain 1066 selected according to litter size at weaning. A more original strategy would consist of selecting strains 1066 and 1077 according to the performance of crossbred does 1067 and 1076. Brun (1984 and 1985) formulated a model of existing interactions between the genotype of a single animal and that of the "partner's population". It was the

generalisation of the concept of interaction between genotype and environment that required the classing of single animals and variability between descendants to be modified. Brun (1984) chose as indicator of this interaction the coefficient of the general aptitude to combine in crossbreeding against the general aptitude to combine within a strain. According to bibliographical sources, a slightly hereditabile character which was sensible to heterosis effects and had been selected for a long timem, helped to make up the conditions favouring the occurrence of an interaction. In this case the correlation between the 2 general aptitudes to combine would be low or negative and there would be a greater rate of genetic additive variability in crossbreeding than within a strain. It would be possible to advance the hypothesis of a connection, not linear in nature, between intra and inter strain additive effects.

## 2) Applied aspects

Genetic improvements constituted a mystery for a lot of rabbit breeders. It was then important to demystify it while showing that it remained the domain of professionally trained experts. At present rabbit breeders can no longer be their own geneticians, even if a good range of articles made serious efforts to vulgarize this domain (Blasco et al., 1984 ; Campo, 1987 ; Randi, 1984 ; Rochambeau, 1984 ; Rouvier, 1983 ; Samoggia, 1985 ; Tsepkon and Mastak, 1984 ; Zucchini, 1986 ; etc.). Although computers provided rabbit breeders with a valuable aid to run their breeding (Gamberini, 1985 ; Masoero, 1984 b), genetics remained a highly complex area.

A description of the schemes for genetic improvements was indispensable to enable rabbit breeders to become properly informed. This was a sphere where anything had yet to be done. The few available articles (Holveck, 1986 ; Le Boucher, 1987 ; Palenzona and Pippa, 1984) were incomplete.

## B. Promoting genetic improvements

### 1) Preliminary remarks

The promotion of genetic improvements obviously implies the existence of genetic improvements to promote. The selection of strains employed in promotion practices remains an indispensable prerequisite, although at present rabbit breeds in France, Italy and Spain are mainly concerned with the sanitary problems related to promoting genetic improvements their animals may suffer. As sanitary problems lose their importance, the main West European rabbit selectors will feel more commercially induced to take an active interest in a swift evolution of genetic differences. A good commercial dynamism and intelligent utilisation of heterosis effects will no longer be sufficient. Matheron and Poujardieu (1984 a) had already raised this problem, but little progress had been done since. One can feel nothing but uneasy as it is learnt that in Northern Italy there was a promotion of sperm pales obtained from strains "selected" according to their health or their aptitude to donate semen. Artificial insemination can considerably promote genetic improvements in rabbit breeding, but only subject to 2 conditions. There were a few technical problems that needed solving first, they would otherwise risk to prevent the achievement of the necessary level of economic profitability if they were not solved on time. It is then necessary to promote the sperm of bucks belonging to coherent genetic schemes. The simplest approach would consist in integrating artificial insemination in existing networks.

During the 70's, pyramid networks for the achievements and promotion of genetic progress were set up in Western Europe. A similar evolution took place with regard to poultry and pigs. The operating principle of these networks was simple : a selector built up a significant amount of genetic achievements in several strains. These strains were selected for specific groups of complementary characters. Some were directed more towards prolificacy and fertility, others towards body growth and gross feed efficiency. That was the last step at the peak of the pyramid in selection ties. The number of animals from these strains were subsequently increased and crossbred within single or multi-level promotion networks. A network was made up of several multiplier herds. The aim was to obtain a buck for terminal cross and a crossbred doe, known as hybrid, which were to be introduced in commercial rearing farms. Commercial rearing farms formed the base of the pyramid. The schemes used to produce important batches of homogeneously performing animals. They played an essential role in the rationalisation of rabbit breeding in Western Europe to an equivalent degree to that granted to the producers of granulated feed

and of other kinds of accessory material necessary for rabbit rearing. These schemes also presented drawbacks. They used to become efficient schemes for the spread of sanitary problems. As trust between rabbit breeders and dealers in animals for reproduction began to weaken, the situation worsened rapidly. Rabbit breeders no longer dared to buy outside animals. They were frightened of possible sanitary difficulties arising from the introduction of new elements within their own animals. There was a strong temptation to carry out self-renewal, which consisted in the utilisation of a female derived from the crossbreeding of a daughter from a terminal cross buck and a hybrid doe. Nevertheless, with reference to the experience of a French breeding farm Roustan et al. (1986) showed that self-renewal brought about a fall in performance. Although rabbit breeders had the impression that this was the least expensive solution, no definitive conclusion should have been reached before a fully fledged economic analysis was carried out. Despite the sanitary and renewal problems investigated, pyramid schemes undoubtedly remained the best available means to obtain and promote genetic achievements for all rabbit breeders who had invested considerable amounts and were after a high level of productivity. An intelligent utilisation of artificial insemination could lead to substantially improving the efficiency of pyramid schemes over the next few years.

However, this model for a rational and intensive production was by no means the only available one in Western Europe or in the world. For systems which, although rational, were based on extensive formulas, the productivity levels aimed at were much inferior. There were other schemes available dealing with the achievement and promotion of genetic progress. It was possible to observe that during the last few years there has been a return to pure breeds in France, Italy and Spain. A simple crossbreeding between two breeds, if well formulated, could provide a breeder with a reasonable rate of productivity and it simplified renewal problems. For other countries wishing to develop rabbit breeding, the importation of a pyramid scheme was not necessarily the best solution. Difficulties of adaptation to local breeding conditions faced by imported animals could constitute a factor limiting considerably the expression of their genetic potential. At each instance a comparison with local rabbit populations should be urged, which could reveal quite surprising results (Matheron and Dolet, 1986). With reference to the project set up in Mexico, selecting local breeds proved worth its while (Lebas et al., 1986).

## 2) Applied aspects

At the Rome Conference the Toulouse team (Roustan and Poujardieu, 1984) had presented a new system to promote the strains they had selected in experimental conditions. This system, known as demultiplication, was analysed in its theoretical implications (Rochambeau and Matheron, 1986). The addition of a supplementary multiplication tier had increased the promoting power of the scheme by a factor of 15. It was also important to check the quality of the animals produced. That was the objective that the Control Committee for Demultiplication, located under the direction of the French Ministry of Agriculture, attempted to obtain (G.I.E. Midi-Pyrénées Lapin, 1986). At the same time the French Producers' National Federation (FENALAP), anxious about the sanitary problems which had appeared in commercial rearing centres proposed a Veterinary Chart for the Production and Utilisation of Breeding Animals

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- These initiatives were stipulated by contract, contrary to what happened in Spain (Catalogne) where there existed legal regulations.
- Breeding animals from different tiers were tattooed and accompanied by a birth certificate.
- Multiplication breeding farm had to keep an individual technical management. Individual technical management had to account for every litter of every doe in the farm. The results were then made available for inspection to the Control Committee. The results from breeding farms being part of the demultiplication networks are presented on Table (25). It is regretted that the size of the sample of commercial breeding farms was so small. These results attempted to take into consideration most of the breeding centres of all recognised networks with regard to demultiplication and multiplication tiers.
- Breeding farms dealing with multiplication were regularly paid visits by a committee of experts who assessed if all necessary conditions were fulfilled to produce high quality breeding animals.
- Following the visit to the breeding farm and having analysed the records kept on each animal, the Committee granted the breeding farm for multiplication a provisional statement of approval. Membership to either of these 2 institutions required the fulfilment of a few more technical obligations. These 2 complementary actions contributed to gradually re-establish confidence between rabbit breeders and farm animal dealers.

However, there existed differences between the 2 institutions. The Demultiplication Control Committee only took into consideration networks as a whole, and it was a whole network that became recognised. On the contrary, the FENALAP took into consideration each individual element making up a network and granted separate certificates to each of them. However, a multiplication breeding site within a network could not be awarded recognition unless the selection breeding farm upon which it depended had already been awarded recognition. It was thought likely that these 2 institutions may be merged in the coming years to give a unified procedure dealing with the recognition of networks operating to obtain and promote genetic progress.

Also the underlying operational principles of the 2 institutions differed on a particular point: their sanitary diagnosis. Morisse, who worked out the setting up of the FENALAP, supposed that the sanitary well-being of a doe was largely determined by that of the litter from which it descended. He then recommended not to breed stud animals from litters reporting a mortality rate above 15 % during the period between birth and weaning. Poujardieu (1986) tested this hypothesis by analysing the productive life of 1500 does with regard to the features of the litters in which they were reared. The 2 factors he considered - litter size at birth, number of dead offspring between birth and weaning - only accounted for 4 % of character overall variability in the productive life of these does. In the conditions of production described by Poujardieu (1986), Morisse's hypothesis could not be convalidated.

### C. Analysis of results from commercial breeding farms

#### 1) General principles

What researchers in applied genetics working on rabbits were aiming at was to increase the animal rate of adaptation with regard to breeders' requirements. These requirements may vary from breeder to

breeder : an actual income in Western Europe, a high quantity meat for self-consumption in Mexico, etc.. To assess the extent this objective had been achieved, it was necessary to take down the data relating to the technical and economic performance from a sample of commercial breeding farms.

The first part of the analysis was concerned with the technico-economic management of the farms. For a pre-determined length of time (for example, a week) breeders reported the number of mating sessions, number of does gone into littering, number of live and still born offspring, number of rabbits at weaning, number of animals sold..., quantity of feed purchased, etc.. Yearly technical and economic results were extrapolated by means of a series of formulas centred round 2 basic units : the doe and the "littering cage" ("cage mère"). Does were zootechnic units the definition of which was clear. "Littering cage" were zootechnic units the meaning of which was a little more complex. A "littering cage" consisted of a cage provided with a nest box. It was not until a long time ago that does spent their whole productive life in the same cage. Since the introduction of "pre-delivery cages" ("cages de pre-cheptel") and "in-between-delivery cages" ("cages d'attente") rabbit keepers have been able to have a higher number of does than "littering cages". The target of this operation was to render investment more profitable. At present "littering cages" do not represent exactly the same thing from one breeding farm to another ; on the whole, a "littering cage" was made up of "pre-delivery" and "in-between-delivery" cages. This confusion made comparison in time and space difficult. Despite these drawbacks, technico-economic managements provided interesting results as it will be seen further on. Several technico-economic managements were established in Spain (Cabrero and Tarafa, 1984 ; Valls, 1986) and in France (Anonimus, 1985 and 1986 ; Henaff et al., 1987, Yoncourt and Nicaud, 1987). Miroshnichenko et al. (1981) further supplied the results from 10 well-run breeding centres in the USSR.

The second approach was concerned with individual technical management, in which the registered unit was the single doe. Every month rabbit keepers recorded all significant information relative to each litter being weaned. Technical results were calculated over variable periods (months, quarters, years, etc.). They were most often expressed "per doe" and occasionally "per littering cage". This was the approach employed in France ("Contrôle de Performances en Ferme INRA-ITAVI") and in Spain (Programa de Control de Rendimientos en Granja). Available results were published more or less regularly (Rafael et al., 1982 ; Rafael, 1984 ; Rafael et al., 1988 ; Anonimus, 1986).

These 2 approaches complemented each other. The first one was simple in nature and could be employed in a large number of breeding farms. The second one was more complex in nature and the number of breeding farms employing it was smaller. This second approach supplied exclusively technical results though more elaborated. The valorisation of these approaches took place at different levels : at breeding farms, networks of breeding farms on a local and national level scale. Resulting files were then used to compile synthetical (Henaff et al., 1986 ; Koehl and Magdelaine, 1986) or more analytical studies (Poujardieu, 1986 ; Roustan et al., 1986 etc...).

## 2) Analysis of results obtained from GILATAP sample between 1974 and 1986

Table 26 presents the evolution of technical and economic results in a sample of French breeding farms between 1974 and 1986. This sample included some well-run breeding farms, but it would be possible to reach much higher standards. The productivity rate per doe has been stagnant since 1982, after having been improved since 1974. This result was the outcome of a shortening of intervals between litters, a rise and then a stabilization of litter size at birth, an increase in pre- and post-weaning mortality rates. Instead, productivity rate per "littering cage" continued to improve as a result of the increase in occupation rate of the cages. However, it has already been pointed out the difficulty of carrying out comparisons over long periods of time, the definition of a "littering cage" having altered between 1974 and 1986. Renewal rate almost doubled during this period. Finally, margins on feed expenditures increased positively between 1974 and 1986, but the rate of increase has been lower than the rate of inflation since 1982.

This short analysis calls upon researchers of genetics applied to rabbit breeding to intervene.

The stagnation of litter sizes at birth was alarming. Was that meant to reflect a lack of selection with the strains employed for reproduction purposes and a generalization of practicing self-renewal ?

The rise in pre- and post-weaning mortality rates was a consequence of degrading sanitary standards within breeding farms. Among the factors contributing to this degradation it was possible to include the uncertain sanitary state in which purchased animals were at times to be found, but also the gradual abandonment on the part of many rabbit breeders of basic hygiene rules and prophylactic measures. However, it must be pointed out that errors in the conception of buildings and equipment used for rabbit breeding considerably complicated some rabbit breeders' task.

The rise in the occupation rate of cages, and the shortening of intervals between littering sessions appeared to produce still now badly assessed zootechnic consequences.

The increase in the renewal rate indicated that does seemed to have difficulties in adapting to the more intensive rhythm of utilization and to the worsening breeding conditions. The productive life of does needed to be studied in its entirety more than ever before.

Since the beginning of the 80's, rabbit breeders' profit margins have progressed in France less fast than inflation. To maintain a stable level of income rabbit breeders have been bound to improve their productivity rate. In what way can genetics give its contribution in the context that has just been outlined?

#### CONCLUSION

##### 1) What are the priorities for geneticists working on rabbits

Since rabbits were animals bred to produce meat, wool or fur, geneticists' ultimate aim was to heighten the animals' adaptation rate to their keepers' requirements and to the environment in which rabbits were reared. In order to fulfil this objective geneticists were bound to consider the best approach to obtain genetic improvements and how to carry out their promotion into commercial rearing centres. To achieve a better understanding geneticists studied simultaneously the genetical and physiological mechanisms determining meat, wool and fur production. The creation and promotion of genetic improvements were often privileged as geneticists were motivated by breaking new efficiency boundaries. The study of the mechanisms nevertheless remained unavoidable to understand and judge to what extent the creation and promotion of genetic improvements was beneficial. Due to their small size and short intervals between generations, rabbits were regarded as an ideal model for the study of genetics in domestic mammals. Rabbits were nevertheless a species of animals by far less well-known than mice, the format of which was significantly less conspicuous. It was therefore necessary to carefully select what seemed to award rabbits a better rating as an ideal study model than any other animal species. Subsequently, it was important to regularly provide researchers involved in the study of other species the results obtained with rabbits and to make sure they were being included in the main bibliographical abstracts. But it was indispensable to call for a true international collaboration because of the low number of teams working on rabbit genetics worldwide.

##### 2) Productivity and reproductive life

Every breeding environment made use of one or several production factors having inevitable side-effects. The supply of stud animals and the promotion of genetic improvements could not be easily guaranteed with regard to breeding farms in developing countries. Environmental features often forced upon the animals hard climatic or nutritional constraints. In European rational breeding investments in site infrastructures and overall equipment were important. Rabbit keepers tended to overlook certain environment factors within their sites (temperature, hygrometry and air flow, etc.) and expected rabbits to adapt. Renewal costs were equally to be fully considered, for rabbit keepers introduced an average number of young new does every year equal to 1.5 the number of pre-existing does.

These few examples show that the reduction of the needs arising from factors limiting production required an outlook going beyond the immediate performance, and called for a study of performances all along a doe's productive life. All events taking place during the period spanning between the moment

ovules were fertilized and the first time does were served were largely responsible for subsequent rates of performance during future does productive life. Nowadays priority is granted to studying the conditions in which bucks and does specifically bred for reproductive purposes ought to be reared. The unity of time to choose to carry out comparisons among different rabbit populations must be their productive life in all its entirety. To limit observations to only one or a few litters can provide contradicting results. Possible interactions with the breeding environment must not equally be neglected. For a comparison between 2 populations to be complete, the analyses should be performed while maintaining the rabbits concerned in their original breeding environments. Both the breeders and the environment they constructed at their rearing sites constituted a series of aggressions forced upon rabbits: intensive reproduction rhythm, unbalanced diets, excessive heat, etc.. To counterattack these aggressions animals activated specific and non-specific means of resistance of differing natures. Performance rating during rabbits' productive life was a good indicator of the degree of adaptation to their breeding environments; that is, their ability to activate their means of resistance.

In the case of Angora rabbits, the primary objective in their productive life was wool production. The productive and reproductive aspects in the life of rabbits were not necessarily connected. The characteristics of the reproductive life of the different breeds of Angora rabbits constituted a factor limiting the creation and promotion of genetic improvements. Artificial insemination opened up interesting new perspectives. However, it must not be forgotten that it also created technical problems - the ratio between the number of live born offspring and the number of bucks volunteered for insemination was still low - and economic problems - how much did it cost to perform artificial insemination employing fresh semen, refrigerated semen and frozen semen? If artificial insemination turned out to be more expensive than natural covering, how far would it be supported?

### 3) Interactions between a gene and the genome in which it found expression, or between 2 genomes

Rabbits were a good model species for the study of these interaction problems. The Rex and Angora genes were 2 major genes determining fleece structure. Studying their effects in different genomes could be easily accomplished thanks to the small size of rabbits and to their short intervals between generations. The analysis did not, and must not, stop with the evaluation of fleeces' features. It included the whole range of production characters (litter size, growth, etc...).

In their rationality, a good number of European breeders made use of cross-bred does. It was therefore tempting to employ a selection scheme of a recurring and reciprocal nature to select basic strains. Using cross-bred does' performances - measured at commercial breeding centres to select basic strains - further permitted to carry out a selection according to the rate of adaptation to breeding conditions at commercial sites.

Having obtained transgenic animals was not an end in itself. Expression and transmission modalities of artificially inserted genes in a new genome were poorly known. To study them a large number of animals would have to be observed. Once more, rabbits appeared a good model to perform the transfer of transgenic animals from the laboratory to commercial breeding centres.

### 4) Assessing the results obtained by teams using rabbits as a biological model

Several teams were studying some very subtle mechanisms operating in rabbits, but their results were seldom assessed by the teams working on rabbits' production. It has just been said that there was a shortage of teams whose members specifically studied the genetical and physiological mechanisms determining meat and wool production in rabbits. Could it not be possible to combine the approaches of these two kinds of researchers? Immunogenetics provided a particularly clear example. Immunity responses constituted an important component of rabbits' response to aggression. Transmission modalities of immunity responses were then to attract the interest of researchers dealing with applied genetics. Indeed, many teams studied rabbit immunology. If the next world conference on rabbits is to take place, as presumed, in the USA, ought not representatives of some of these teams be invited? This attempt of openness should also be applied to other disciplines.

Rabbits belong to a small animal species with regard to both their size and economic importance. To make the best of their small size without being too conditioned by their limited economic importance, researchers in applied genetics ought to adopt a more open approach towards other disciplines. This opening demanded the creation of a dialogue among the teams who were operating in different countries, but also with geneticists dealing with other species of domestic animals, as well as specialists in other disciplines taking an interest in rabbits, and teams using rabbits as as biological model.



Table A - Abbreviations of the name of breeds and strains used in the tables

BOG : Bouscat Giant	MRC : Moravian Giant
BUF : Burgundy Fawn	NZW : New Zeland White
BLG : Baladi Grey	PAL : Palomio
BLR : Baladi Red	PZG : Pezzata giant
BLY : Baladi Yellow	RAN : Russian Angora
BRG : Bourbonais Grey	RUS : Small Russian
CAL : Californian	SAN : Sandy
CHI : Chinchilla	SCH : Soviet Chinchilla
CZW : Czech Albino	TRC : Turingia Chamois
DNW : Danish White	TRW : Termonde White
DUT : Dutch	VNB : Vienna Blue
FGW : Flemish Giant White	VNW : Vienna White
FOW : Florida White	CUN : Cunistar
FRS : French Silver	ELC : Elco
GCH : Giant Chinchilla	HYL : Hyla
GGR : Giant Grey	NOR : Norfolk
GWH : Giant White	PRO : Provisal
GZW : Giza White	RVK : RVK White
	SOL : Solaf
	ZIK : Zika

Table B - Abbreviations of the name of traits used in the tables

<u>LS : Litter size</u>	ADF : Average daily food
TLS : Total litter size	ADG : Average daily gain
BLS : Birth litter size	FCR : Feed conversion ratio
WLS : Weaning litter size	GFE : Gross feed efficiency
SLS : Slaughter litter size	LFE : Litter feed efficiency
XLS : Litter size at x weeks	TGR : Total growth rate
	DRP : Dressing percentage
<u>LW : Litter weight</u>	FTP : Fat percentage
WLW : Weaning litter weight	KDF : Kidney fat
	LNP : Lean percentage
	MBR : Meat/bone ration
<u>IW : Individual weight</u>	
WIW : Weaning individual weight	
SIW : Slaughter individual weight	
XIW : Individual weight at x weeks	
AIW : Adult individual weight	
PWG : Post weaning growth	

Table 1 - Numbers of papers per theme and per country about Angora rabbits' genetics

	Bulgaria	Chili	China	Czechosl.	Denmark	France	Ger. Fed. Rep.	Hungary	India	Italy	Poland	USA	TOTAL
Factors of variation	1	8	-	-	-	2	1	-	-	-	1	-	13
Genetical evaluation of breeds	-	-	3	1	1	-	13	-	2	-	-	-	20
Fertility and fecundity	-	1	3	-	-	-	5	2	-	-	-	-	11
Miscellaneous	-	-	1	-	-	4	1	-	1	1	1	1	10
Total	1	9	7	1	1	6	20	2	3	1	2	1	54

Table 2 : Differents types of Angora rabbit hairs (from ROUGEOT and THEBAULT, 1984b)

Types of hair	Tylotrichs	Bristle	Awn	Down
Length	12-13 cm	10-11 cm	8,5 cm	7,5 cm
Head diameter	100 m	90-100 m	60-80 m	-
Trunk diameter	60 m	50-60 m	16-30 m	15 m
Hair-producing follicle	Central primary	Central primary	Lateral primary	Secondary

Table 3 - Effect of the number of harvest on wool yield

Authors	Number of harvest						Remarks
	1	2	3	4	5->8	9->	
ROUGEOT and THEBAULT, 1984a	18	58	73	100 =225g	117	93	Plucking
MAGOFKE et al, 1982b	20	75	90	100 =144g			Shearing
MAGOFKE et al, 1978	10	54	100 =259g				Shearing
RICKE MUNOZ, 1984			100 =153g		85	84	Shearing
OCETKIEWICZ and TUCZYNSKA, 1981			100 =455g		124	143	Shearing Annual yield/wool
ROCHAMBEAU and THEBAULT, 1988	11	65	87	100 =230g	108	104	Plucking

Table 4 - Effect of sex on wool yield

Authors	Wool yield of the does	Wool yield of the bucks in %	Remarks
ROUGEOT and THEBAULT 1984a	100 = 955g	80	Plucking Annual wool yield
MAGOFKE et al, 1982b	100 = 114g 100 = 144g 100 = 144g	91 93 95	2nd harvest 3rd harvest 4nd harvest
from SCHLOLAUT, 1987	100 = 630g 100 = 870g 100 = 1050g 100 = 1200g	89 89 88 85	1960 1970 Annual 1980 wool 1985 yield
BAYERISCHE 1982 ----> 1987	100 = 1126g	89	Annual wool yield
LANDSANSALT, FINGERLAND 1980	100 = 1100g	85	Annual wool yield
JELINEK et al, 1980	100 = 135g 100 = 139g	83 90	2nd harvest 3rd harvest
OCETKIEWICZ and TUCZYNSKA, 1981	100 = 455g	100	Annual wool yield
RICKE MUNOZ, 1984	100 = 142g	92	Various numbers of harvest

Table 5 - Correlations between number of harvest, live weight and wool yield

Authors		Number of harvest				Remarks
		1	2	3	4	
MAGOFKE et al, 1982b	Live weight	40	87,5	92,5	100=3348g	Shearing - 4th wool yield=144g
RICKE MUNOS and MAGOFKE, 1982	Phenotypic corr.	0,73	0,64	0,49	0,15	
THEBAULT, and ROCHAMBEAU, 1988	Live weight	38	80	90	100=3826g	Plucking 4th wool yield=230g
	Phenotypic corr.	0,72	0,35	0,18	0,29	

Table 6 - Effect of birth litter size and individual live weight and wool yield  
(from MAGOFKE et al, 1982a and b)

Litter size	Individual weaning weight	1rd harvest		2nd harvest		3rd harvest		4th harvest	
		Live weight	wool yield	Live weight	wool yield	Live weight	wool yield	Live weight	wool yield
< 3	100 = 1022g	100 = 1715g	100 = 31g	100 = 2974g	100 = 117g	100 = 3777g	100 = 147g	100 = 3547g	100 = 148g
4	82	94	90	98	101	93	100	95	103
5	75	90	86	97	99	93	98	95	99
6	65	85	84	93	93	90	98	91	95
> 7	63	82	80	92	95	90	95	91	96
signifi- cation	*	*	*	*	*	*	NS	*	NS

Table 7 - Effect of season of harvest on wool yield

Authors	Winter	Spring	Summer	Autumn	Remarks
ROUGEOT and THEBAULT, 1984b	110	102	80	107	100 = 215g Plucking
KETTNER, 1962 from ROUGEOT and THEBAULT, 1984b	100	97	97	106	Shearing
CHARLET-LERY et al, 1985	104	100	94	101	100 = 246 g Plucking
MAGOFKE et al, 1982b	111	101	88	100	100= 27g(1st harvest) 100=144g(4th harvest)
THEBAULT and ROCHANBEAU, 1988	107	101	79	103	1st harvest, plucking 100 = 35g
	112	104	90	103	2nd harvest, plucking 100 = 149g
	101	97	90	117	3rd harvest, plucking 100 = 200 g
	101	98	102	102	Others harvest, plucking 100 = 242 g

Table 8 - Phenotypic correlations between the first four wool yield.  
Heritability of wool yield and of live weight

Phenotypic correlation	1st harvest	2nd harvest	3rd harvest	4th harvest
1st harvest		0,16	0,06	0,10
2nd harvest			0,35	0,20
3rd harvest				0,54
=====				
H <sup>2</sup> of wool yield	0,20 ± 0,12	0,23 ± 0,12	0,09 ± 0,12	0,08 ± 0,20
=====				
H <sup>2</sup> of live weight	0,47 ± 0,15	0,72 ± 0,19	0,67 ± 0,20	0,29 ± 0,22

Table 9 - Heritabilities and genetic correlations among performance trait  
in Australian feral goats (RESTALL et al, 1984 quoted by  
MILLIAR, 1986)

	Undercoat weight	Undercoat diameters	Undercoat length	Growth rate	Body weight at 18 months
Undercoat diameter	0,97±0,16				
Undercoat length	0,80±0,18	0,74±0,24			
Growth rate	-0,69±0,48	-0,51±0,44	-0,85±0,44		
Body weight at 18 months	-0,57±0,45	-0,94±0,36	-0,55±0,44	0,79±0,32	
Heritability	0,59±0,37	0,77±0,39	0,93±0,41	0,56±0,36	0,68±0,34

Table 10 - Data from 10 wool performance tests on Angora rabbits  
(BAYERISCHE LANDESANSTALT FÜR TIERZUCHT, GERMAN FEDERAL REPUBLIC)

Years of publication	1982		1983		1984		1985		1987	
Test Number	37th	38th	39th	40th	41th	44th	45th	46th	47th	48th
Number of does	33	28	41	14	27	18	26	12	22	14
Estimated annual wool yield	1211g	1138g	1116g	1109g	1171g	1237g	1061g	994g	1090g	1132g
Live weight of the does	3480g	3590g	3600g	3540g	3760g	3890g	3600g	4100g	4010g	4300g

Table 11 : Breeds comparison on wool yield  
(CA : Chinese Angora ; FA : French Angora ; GA : German Angora)

Authors	Traits	Breeds			
		CA	GA	FAxGA	GAxFA
GARCIA et al, 1984	Annual wool yield	93	100 - 505g		
	Live weight	107	100 - 3287g		
DAI et al, 1985	Annual wool yield	62	100 - 422g	91	84
	Hair diameter	115	100 - 12,2µm	95	93
GAO et al, 1983	Annual wool yield	100	GAxCA 137	GA (GAxCA) 227	GAx(GAx (GAxCA)) 221

TABLE 12 : Breeds comparison on litter size  
(GA : German Angora ; LA : Griollo Angora)

Authors	Traits	Breeds			
		LA	GA	GAXLA	LAXGA
GARCIA et al, 1984	Birth litter size	106	100 - 3,92	145	142
	Weaning litter size	77	100 - 3,33	120	117
THEBAULT and ROCHAMBEAU, 1988 (French Angora)	Birth litter size	4,90			
	Adjusted litter size	3,18			
	Weaning litter size	2,38			

Table 13 - Numbers of papers per theme and per country about meat rabbit's genetics

	EUROPE										AMERICA				ASIA			AFRICA												
	BELGIUM	CZECHOSLOVAKIA	DENMARK	FRANCE	GERMAN DEM. REP.	GERMAN FED. REP.	GREAT BRITAIN	HUNGARY	ITALY	POLAND	SPAIN	SWEDEN	SWITZERLAND	THE NETHERLANDS	USSR	YUGOSLAVIA	BRAZIL	CANADA	CUBA	USA	INDIA	INDONESIA	JAPAN	PEO. REP. CHINA	TAIWAN	EGYPT	TANZANIA	TURISIA	AUSTRALIA	TOTAL
Books	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	5
Biochemical polymorphisms and coat and color genes	0	1	0	1	0	2	0	1	3	0	9	1	0	1	3	0	0	0	0	1	0	0	1	0	0	0	0	0	0	24
Genes, chromosomes and immunogenetics	0	0	0	8	0	3	3	0	0	0	2	1	5	0	2	0	0	2	0	27	0	0	2	0	0	0	0	1	0	54
Selection and spreading	3	4	1	22	1	0	0	0	0	1	9	0	0	0	2	0	0	0	1	3	0	0	0	0	0	0	2	0	0	56
Mechanism and genetic parameters	2	2	0	12	0	1	0	2	8	0	5	0	0	0	4	0	0	0	0	0	2	0	0	1	1	2	0	0	1	35
Selection experiments	0	0	0	1	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	1	6	0	0	0	0	0	2	0	0	14
Investigation on populations	0	3	0	8	1	0	1	0	4	4	5	0	0	3	2	0	0	0	0	1	0	1	0	2	0	0	0	0	0	35
Comperison of populations	5	9	3	3	0	2	0	0	10	3	2	0	0	0	6	2	3	0	1	5	7	1	0	0	0	0	7	0	0	69
Results of production herds	0	0	0	5	0	0	0	0	0	0	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Total	10	19	4	61	3	9	4	3	25	8	40	2	5	4	21	2	3	2	2	40	15	2	3	3	1	11	2	1	0	302



Table 14 - Some biochemical polymorphism in rabbits  
(LG : linkage group ; Chr : chromosome)

Symbol	System	Localization
Ada	Adenosin Denamisase	
Ca2	Anhydrase Carbonic 2	
Es1	Esterase 1	LG VI
Es2	Esterase 2	LG VI
Es3	Esterase 3	
Es7	Esterase 7	
Est 4	Seric Esterase	LG VI
	Å globulin	
	Hapto globulin	
HbÁ	Hemoglobin Á	
Hp	Hemopepsin	
Hx	Hemopexin	Chr 1
	Postalbumin	
6 Pgd	6 Phosphogluconate deshydrogenase	Chr X
Prt	Plasma transferine	LG VIII
RL-A	Major histocompatibility complex	LG VII
Tf	Transferin	

Table 15 - Linkage map of the rabbit (LG : linkage group ; Chr : chromosome  
U : isolated genes)

: Chr 1	: A2M, ACP2, B, C, GALT, HB $\bar{A}$ , HQ, HU, HX, LDH-A, UGL1, Y.	:
:	:	:
: Chr 4	:	:
: or 14	: GAPD, LDH-B, TPI1.	:
:	:	:
: Chr 9	: AGY1, GFX1.	:
:	:	:
: Chr 12	: CAS-A, CAS-B.	:
:	:	:
: Chr 13	: PGM1.	:
:	:	:
: Chr 15	: GUK1, IGK, LPQ-A, LPQ-B, LPQ-C, MDH2, PRI.	:
:	:	:
: Chr 16	: IGH, ITPA, NP, PEPB.	:
:	:	:
: Chr 19	: GSR.	:
:	:	:
: Chr X	: 6 PGD, GLA, HPRT, PGK, PT.	:
:	:	:
: LG II	: DU, EN, L.	:
:	:	:
: LG III	: R1, R2.	:
:	:	:
: LG IV	: A, DW, HG, W.	:
:	:	:
: LG V	: AN, BR, F, HB.	:
:	:	:
: LG VI	: E, ES1, ES2, EST1, EST2, EST4, EST6.	:
:	:	:
: LG VII	: HE, RL-A, SA.	:
:	:	:
: U1	: PGD.	:
:	:	:
: U2	: ENO1.	:
:	:	:
: U5	: MDH1.	:
:	:	:
: U6	: GPI.	:
:	:	:
: U7	: HBA.	:
:	:	:
: B1	: PEPS.	:

Table 16 - Some experiments of production of transgenic rabbits by microinjection

AUTHORS	BREM et al, 1985 and 1986	BUHLER et al, 1987	HAMMER et al, 1985	STROJEK 1986
Gene	MT - hGH	IgM	MT - hGH	CAT-Uteroglobin
Number of manipulated eggs	385	258	1907	805
Foetus		11		
Stillborns	37	4	218	37
Alive rabbits		6		
Number of transgenic rabbits	5 from 27	?	28	10
Expression frequency	?	?	4 from 16 (mRNA) 1 from 1 (serum)	?

Table 17 - Breakdown of the does in the French rabbit herds by strains or by breed in % from a survey of the Agriculture Ministry : SCES, 1982).

Bread or strain	ALL the herds	Herds belonging to a production group
Hyla	17	38
Solaf	5	14
Elco	2	5
Jary	1	1
Others hybrids	49	49
New Zealand White	8	13
California	3	3
White Bouscat Giant	3	1
Burgundy Fawn	3	1
Butterfly Giant	2	-
Flemish Giant	1	-
White Vendée	1	-
Small Russian	1	-
Great Russian	1	-
Others breeds	3	2

Proceedings 4th World Rabbit Congress, 10-14 October 1988, Budapest Hungary, Vol. 2, 1-68

Table 16 - Breakdown of comparison between breeds and strains by traits

	BREEDS																				STRAINS												TRAITS																	
	ENG	BLY	MAC	BRF	CAL	CHI	DWI	OUT	FAY	FAL	FIS	CG	GR	GU	COU	YEM	FIN	PAL	RAJ	RUS	CH	TPC	TRJ	WE	VNI	CHN	TSC	AVL	WR	MO	NS	SP	ZIK	CO	GE	LE	LY	SP												
GHEM RES. CENT., 1984																											X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X								
AFIFI and EHARA, 1987	X	X						X							X																									X	X	X	X							
AUTILIA and MASOERO, 1986				X	X																																				X	X	X	X						
BARGE and MASOERO, 1986				X	X																																					X	X	X	X					
BLASCO et al, 1983				X	X																																						X	X	X	X				
BOCCIAGNONE et al, 1983				X	X																																							X	X	X	X			
BRUN and ROUVIER, 1984				X	X																																								X	X	X	X		
GARREGAL, 1981				X	X			X																																				X	X	X	X			
DANKDAR and JAKTAR, 1985																																													X	X	X	X		
DELSAVO and ZUCCHI, 1984				X	X							X																																	X	X	X	X		
GRANDI and STEFANETTI, 1987				X	X																																								X	X	X	X		
GROHNER et al, 1985				X	X																																									X	X	X	X	
GUGUSKIVILI, 1981				X	X																																									X	X	X	X	
KHALI et al, 1987				X	X																																									X	X	X	X	
KOSBA et al, 1985	X	X	X																																											X	X	X	X	
LANIRI and MAHAJAN, 1983 and 1984				X	X																																										X	X	X	X
LANGE, 1986				X	X																																										X	X	X	X
LUKEFARR et al, 1983 and 1984				X	X																																									X	X	X	X	
LUKEFARR et al, 1984				X	X																																									X	X	X	X	
MACH et al, 1983				X	X																																									X	X	X	X	
MACH et al, 1986				X	X																																									X	X	X	X	
MACH et TROJAN, 1986				X	X																																									X	X	X	X	
MASOERO et al, 1985				X	X																																										X	X	X	X
HIROPSHICHENKO et al, 1981				X	X																																									X	X	X	X	
NIEDZMIADEK and KAWINSKA, 1982				X	X																																									X	X	X	X	
NIEDZMIADEK et al, 1983				X	X																																									X	X	X	X	
NWIEZ et al, 1985				X	X																																									X	X	X	X	
PERRIER and CHEVALIER, 1984 and 1986				X	X																																									X	X	X	X	
PILANDON et al, 1986				X	X																																									X	X	X	X	
PONCE de LEON and MENCHACA, 1985				X	X																																									X	X	X	X	
RAMMATHULLA et BHV., 1986				X	X																																									X	X	X	X	
RODERO et al, 1986				X	X																																										X	X	X	X
RODECHA and CHAMPONGSANG, 1986				X	X																																									X	X	X	X	
SABBION and CANDEO, 1987				X	X																																									X	X	X	X	
SAFOROVA and TROJAN, 1982				X	X																																									X	X	X	X	
TINAEV, 1984				X	X																																									X	X	X	X	
TROJAN and MACH, 1982				X	X																																									X	X	X	X	
ZELNIK and RAFAY, 1986				X	X																																									X	X	X	X	
CHIERICATO and FILOTTO, 1988				X	X																																									X	X	X	X	
KOSBA and ABO EL-EZZ, 1988	X	X	X																																											X	X	X	X	
KOCHNO et al, 1988				X	X																																									X	X	X	X	
BRUN and CUNATOLU, 1988				X	X																																									X	X	X	X	

Table 19 - Breeds and strains comparisons on litter size

AUTHORS	BREEDS						STRAINS			HETEROSIS
	Traits	CAL	NZW	BOG	GGR	SCH	HYL			
								CUN	RUK	ELC
GHEM RES. CENTER	BLS						109	:8,1=100	106	
1984 a et b	WLS							:6,2=100	102	
Belgium	BLS						111	:112:7,3=100	118	
	WLS				GZW		120	:121:5,6=100	120	
								FGW	BLR	
AFIFI and AMARA	BLS			:5,7=100		:116: 99: 93				+ 10 %
1987, Egypt	WLS			:3,7=100		:123:115:100				+ 10 %
								RUS		
BRUN and ROUVIER	BLS	:103	:7,1=100			:88				
1984, France	WLS	:106	:6,2=100			:90				
	WLW	:99	:3,5=100			:69				
DAMODAR and JATKAR	BLS		:4,9=100		:116					
India, 1985	3LS		:4,2=100		:61					
GRANDI and STEFANETTI	BLS	:97	:7,3=100							
1987, Italy										
								PAL		
GROBNER et al.,	BLS		:9,4=100			:86				
1985, USA	WLS		:7,6=100			:80				
GUGUSHVILI	BLS	:83	:8,0=100		:95:100					
1981, USSR										
								GZW		
KHALIL et al.,	BLS			:6,5=100		:98				
1987, Egypt	WLS			:4,9=100		:95				

						:GWH:RAM:				
: LAHIRI and MAHAJAN,	: BLS	: :7,8=100	:	:134:102:111:	:					< 0
: 1983 and 1984, India	: WLS	: :4,8=100	:	:115:111:141:	:					< 0
:	: BLW	: :6,4=100	:	:100: 93:105:103:	:					< 0
:	: WLS	: :4,0=100	:	:114:111:104:121:	:					< 0
									:ZIK:	
: LANGE, 1986	: BLS	: :8,2=100	:		:	107	:		:105:	
: German Federal Rep.	: WLS	: :7,3=100	:		:	103	:		:103:	
						:FLG:				
: LUKEFAHR et al.,	: BLS	: 90 :8,9=100	:		:					+ 10 %
: 1983 and 1984, USA	: WLS	: 85 :6,9=100	:		:					+ 12 %
:	: BLS	: :10,9=100:	:		:	91:	:			
:	: WLS	: :9,2=100	:		:	82:	:			
: MACH	: BLS	:131 :6,6=100	:		:					+ 16 %
: 1986, Czechoslovakia	: WLS	:122 :6,2=100	:		:					+ 12 %
						:DNW:				
: NIEDZWIADK and	: WLS	:106 :5,1=100	:		:	86:	:			
: KAMINSKA,1982, Poland:										
						:NOR:				
: NUÑEZ et al.,	: BLS	: 93 :5,9=100	:		:	104:	:			
: 1985, Brazil	: WLS	:107 :3,6=100	:		:	95:	:			
						:FRS:				
: PERRIER and CHEVALIER:	: TLS		:		:	101:	:8,6=100:			
: 1984, France	: WLS		:		:	80:	:6,5=100:			
						:BRG:				
: PILANDON et AL.,	: TLW		:		:	89:	:8,3=100:			
: 1986, France	: WLS		:		:	93:	:6,6=100:			
						:SAN:				
: RAMMATHULLA and-	: TLS	:5,9=100	:		:	90:				
: BHUVANAKUMAR, 1986	: BLS	:5,3=100	:		:	94:				
: India										
: SABBION and CANDEO,			:		:					
: 1987, Italy			:		:					

Table 20 - Breeds and strains comparisons on postweaning growth

AUTHORS		BREEDS								STRAINS				Observations
	Traits	CAL	NZW	BOG	FRC	FLG				HYL				
GHENT RES. CENTER	WIW									ELC:RUK	CUN:			
1984, Belgium	ADG									790=100: 94:100				
	FCR									34=100:103: 96 :100:				
	DRP									4,0=100: 92:102 :103:				
										63=100: 98: 98 : 99:				
AUXILIA and MASOERO	SIW	98	2,6=100		107:	110			BUF:VNB:PZG:TRC:					Buck
1986, Italy	DRP	100	61=100		103:	100			101:104:105:102:					Strain
	KDF	89	31=100		101:	66			103:102: 98:102:					
	MBR	100	4,5=100		98:	94			89: 72: 65:100:					
									98: 96: 93: 98:					
DAMODAR and JATKAR	10IW		1,9=100						GGR:					
India, 1985									115:					
DESALVO and ZUCCHI	13IW	110	2,3=100		101:				VNB:					
1984, Italy	DRP	102	54=100		105:				128:					
									101:					
GRANDI and STEFANETTI	11IW	101	2,3=100											
1987, Italy	FCR	102	3,4=100											
GROBNER et al.,	WIN		540=100						PAL:					
1985, USA	ADG		35=100						80:					
									89:					
KHALIL et al.,	WIN		440=100:						GZW:					
1987, Egypt	12IW		1,0=100:						98:					
									102:					
KOSBA et al.,	9IW		630=100:						CHI:BLY:					
1985, Egypt	13IW		1,1=100:						111: 67:					
									97: 78:					

Proceedings 4th World Rabbit Congress, 10-14 October 1988, Budapest Hungary, Vol. 2, 1-68

									:ZIK:		
		: AIW :	:4,3=100 :						100	:113:	
: LANGE,	:	: ADG :	: 38=100 :						108	:126:	
: 1986, German Fed. Rep.:	:	: FCR :	:3,3=100 :						101	: 90:	
	:	: DRP :	: 58=100 :						101	: 99:	
		: 22IW :	:3,9=100 :		: 134 :						:Buck
: LUKEFAHR et al.,	:	: WIW :	:560=100 :		: 115 :						:Strain
: 1984 , USA	:	: SIW :	:1,6=100 :		: 115 :						
	:	: LFE :	:0,33+100:		: 100 :						
								:BUF:UNB:			:Buck
: MASOERO et al.,	:	: 5IW 94 :	:780=100 :		: 18: 113 :				:110:107:		:Strain
: 1985, Italy	:	: ADG 106 :	: 32=100 :		:113: 130 :				:113:116:		
	:	: FCR 100 :	:4,4=100 :		: 95: 87 :				: 95: 95:		
								:DNW:			
: NIEDZWIADZECK et al.,	:	: 12IW 100 :	:2,1=100 :		: 93 :						
: 1982, Poland	:	: GFE 100 :	: 100 :		:100:						
								:NOR:			
: NUMEZ et al.,	:	: 8IW 98 :	:1,6=100 :						:102:		
: 1985, Brazil	:	: 12IW 107 :	:2,8=100 :						:114:		
		: 4IW :						:580=100:			
: PERRIER et al.,	:	: 10IW :						:1,9=100:			
: 1986, France	:	: ADG :						: 32=100:			
								:BRG:			
		: AIW :			: 88:			:4,1=100:			
: PILANDON et al.,	:	: 4IW :			: 80:			:630=100:			
: 1986, France	:	: 11IW :			: 93:			:2,3=100:			
	:	: ADG :			: 97:			: 35=100:			
	:	: DRP :			:107:			: 62=100:			





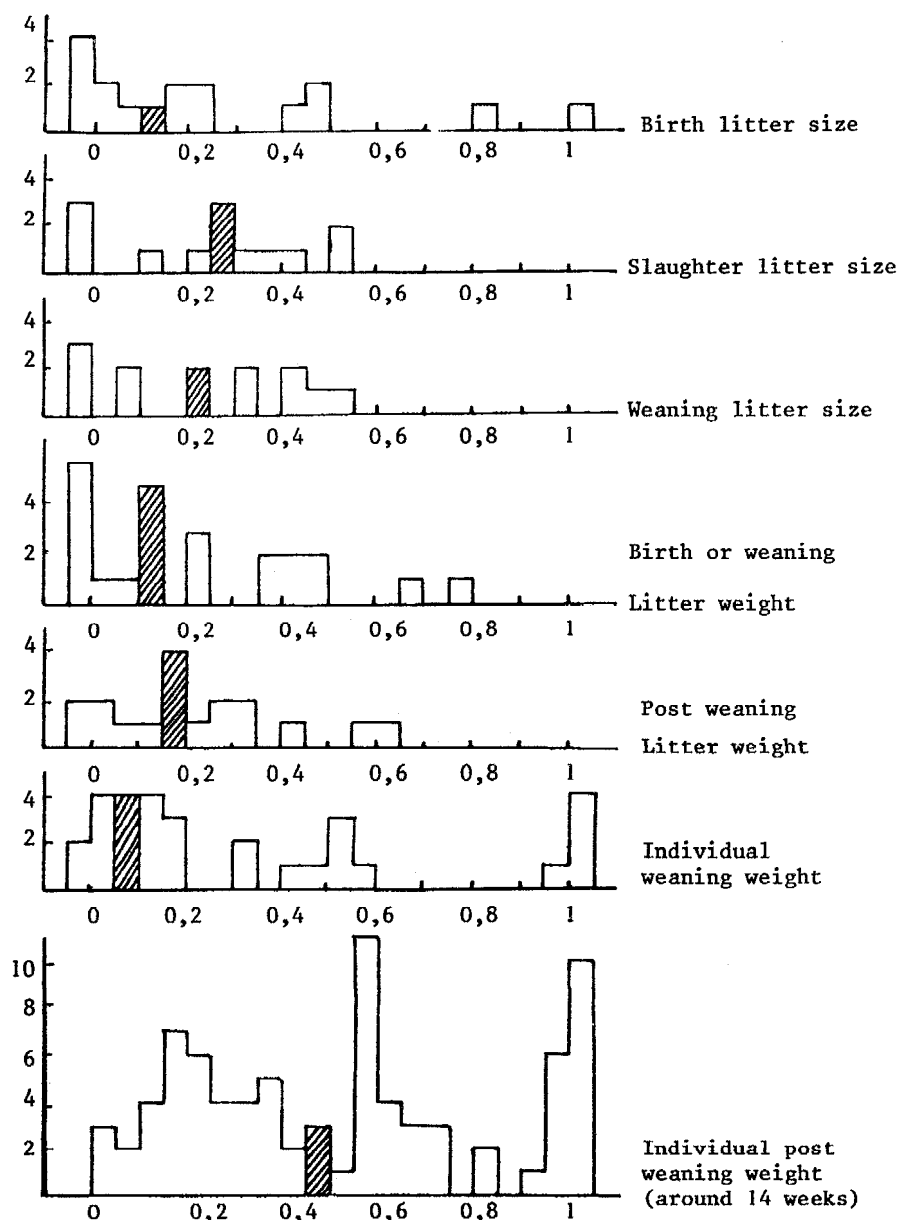


Table 21 - Distribution of estimations of the heritability for some production traits

Table 22 - Estimation of the heritability of some traits

AUTHORS	TRAITS	HERITABILITY
BEROVIDES and FERNANDEZ, 1982	Nest building ability	0,24
HUANG, 1987	Skull measurements	from 0,4 to 0,6
MAHAJAN and LAHIRI, 1983	26 weeks individual weight	0,29 ± 0,03
	Carcass weight	0,14 ± 0,05
	Dressing percentage	0,14 ± 0,02
	Fresh pelt weight	0,10 ± 0,05
PATRAS, 1985	Birth litter size	0,22
	Milk production	0,31
	Birth individual weight	0,48
	9 weeks individual weight	0,54
	13 weeks individual weight	0,62
	17 weeks individual weight	0,59
	Peak body weight	0,53
	26 weeks individual weight	0,66
	Teat number	0,89
	Age peak body weight	0,57
VAREWYCK et al, 1986	Dressing percentage	0,34±0,20 0,70±0,38
	Thigh + loin percentage	0,54±0,26 0,50±0,32
	Thigh meat/bone ratio	0,65±0,28 0,41±0,30
	Loin meat/bone ratio	0,54±0,26 0,28±0,24
CASTELLINI et PANELLA, 1988	Mean 2 weeks individual w.	0,46 maternal
	Weaning individual weight	0,78
	10 weeks individual weight	0,56 components
BASELGA et al, 1988	Score for lung injury	from 0,07 to 0,18
	Mean score for lung injury	from 0,12 to 0,28
MIROSHNICHENKO, 1984	Coat density	0,41

Table 23 - Results of some selection experiments on litter size (D = Does, B = Buck)

AUTHORS	Selection Criterion	Population size	Number of generations	Genetic Trend	Realised Heritability	Selection intensity	Correlated response
MATHERON et al.	WLS	121 D	8	0,08	0,15	0,22	TLS : 0,14 ± 0,0
POUJARDIEU, 1984		33 D		± 0,23	± 0,45		BLS : 0,15 ± 0,19
Strain 1077	index			Control			
ESTANY et al.	WLS	120 D	7	0,05			TLS : 0,04 ± 0,01
Strain A		24 B		± 0,01			BLS : 0,05 ± 0,01
	Index			BLUP			SLS : 0,06 ± 0,01
							IWV : + 2,3 g
							ISW : + 10,3 g
							TGR : + 10,8 g
Strain V	WLS	120 D	1	0,16			IWV : - 5,5 g
		24 B					ISW : - 10,4 g
	Index			BLUP			TGR : - 3,3 g
MGHEMI et al.	s+ : WLS	40 D	4	0,35±0,17	0,22	0,44	
CHRISTENSEN, 1985		20 B					
	s- : Mass			-0,43±0,18	0,30		
				Control	0,26		
NARAYAN et al., 1985	14LS	110 D	6	- 0,05			
		22 B		± 0,05			
	Mass			Control			

Table 24 - Results of some selection experiments on growth rate

AUTHORS	Selection Criterion	Population size	Number of generations	Genetic Trend	Realised Heritability	Selection intensity	Correlated response
FUENTE et al (1986)	ADG Mass	60 D 12 B	8	0,83 g control	0,23	0,93	BLS : - 0,09 SLS : - 0,12
MGHENI et al	s+ : 112 IW	40 D 20 B		+ 52 g	0,11	1,42	
CHRISTENSEN (1985)	s- : Mass		4	- 75 g control	0,31 0,19	1,14	
ESTANY (1987)	TGR	80 D 16 B	6	33			IWW : + 5 ISW : + 30 TLS : + 0,04 BLS : + 0,04 WLS : + 0,05 SLS : + 0,05

Table 25 - Litter size in various tiers of "demultiplication" networks from the INRA experimental strains (NL : number of litters ; \* : estimation from incomplete data )

Tiers	Demultiplier				Multiplier				Commercial				
Strain	1077				1066				Buck 1066 x Doe 1077 ; Terminal buck x Doe 1067				
Year	NL	TLS	BLS	WLS	NL	TLS	BLS	WLS	NL	TLS	BLS	WLS	
1985	4101	8,9	8,3	7,3	970	9,1	8,3	6,9	20490	9,2	8,8	7,7	2415: 9,5 : 9,0 : 8,2
1986	5582	8,8	8,1	6,9	1356	9,0	8,2	6,8	28170	9,2	8,7	7,5	9615: 8,9 : 8,3 : 6,9
1987 *	5722	8,8	8,3	6,9	1332	8,7	8,0	6,8	24840	8,9	8,5	7,5	14487: 8,9 : 8,4 : 7,2

Table 26 - Results of the technical and economical GITALAP managements between 1974 and 1986 (HENAFF et al, 1987).

Trait	Year	1974	1982	1986
Fertility rate (%)		57	66	69
Interval between two litters (days)		69	52	43
Birth litter size		7,2	7,7	7,8
Mortality rate from birth to weaning (%)		19	18	24
Mortality rate from weaning to slaughter (%)		8	11	11
Number of rabbits produced per doe and per year		29	40	40
Does renewal rate (%)		83	125	140
"Cage-mere" employment rate (%)		85	103	115
Number of rabbits produced per "cage-mere" and per year		25	39	46
Gross feed efficiency		4,5	4,3	4,3
Price of the pelleted feed (Francs)		0,78	1,47	1,70
Price of one kg of alive rabbit (Francs)		5,40	12,04	13,72
Profit on feed costs per "cage-mere" and per year (Francs)		131	517	635
Inflation rate (INSEE)		100	233	299

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