HE FUTURE ROLE OF MOLECULAR GENETICS IN THE CONTROL OF MEAT PRODUCTION AND MEAT QUALITY

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UMMARY

Current applications of quantitative genetics for genetic improvement of farm animals rely on sophisticated statistical ocedures applied to fairly simple genetic models and have been effective in producing large cumulative genetic changes in any traits. Recent advances in molecular genetics provide a potential for renewed methods in animal breeding. The two main ssible fields of application of recombinant DNA methodologies, i.e. marker-assisted breeding and gene transfer, are viewed. Use of genetic markers as an aid to present breeding practice appears to be rather promising, but research effort mains to be done before implementation of marker-assisted breeding schemes to a significant scale. It is not, at this stage, vious that transgenesis will be an important way of improving meat-producing animals, at least in the near future.

TRODUCTION

To date, genetic improvement of farm animals has been essentially based on the theory of quantitative genetics. Most its of economic importance (e.g. growth rate, lean content, meat colour) show a continuous phenotypic variation explained a variety of genetic and environmental factors. At the genetic level, it is assumed that a quantitative trait is influenced by merous loci which have individually small effects relative to the total variation of the trait. These loci are termed quantitative it loci or QTL (GELDERMANN, 1975). Under this assumption of polygenic mode of inheritance, it is not possible, in general, determine the genotype of a particular animal by examination of the phenotype alone. Current selection methods rely on a ometrical-statistical approach dealing with the effects of "ghost" genes and not with the genes themselves, and it could be id that animal breeding, though refering to a Mendelian dogma, has a Galtonian liturgy (HANSET, 1989).

The discovery of a number of single major genes with identifiable effects on quantitative traits, as well as recent vances in the field of molecular genetics, offer new prospects for the conversion of polygenic quantitative variability into dividually defined Mendelian entities (BECKMANN and SOLLER, 1987). As far as animal breeding methods are concerned, nefits can be potentially taken from recombinant DNA technology in essentially two manners :

(1) using cloned DNA sequences as probes to uncover genetic variation at the DNA level and for instance adding formation provided by molecular markers of QTL's to that based on usual performance records in selection decisions rker-assisted selection),

(2) inserting cloned foreign genes into the germ line of an animal, for subsequent expression of the inserted gene in the ost and transmission to offspring (transgenesis).

These two applications will be considered in turn in this report. Minimum consideration will be given to purely technical spects and emphasis will be put on the possible future role of these new techniques for increasing rates of genetic progress animal breeding programmes.

- UTILIZATION OF GENETIC MARKERS

1.1. Genetic variation of quantitative traits

- Heritability

For a given trait, heritability (h^2) is the proportion of the total phenotypic variance due to additive effects of all QTL's flecting the trait : $h^2 = \sigma^2_A/\sigma^2_P$ (σ^2_A = additive genetic variance ; σ^2_P = phenotypic variance). The accuracy of the timation of an individual's breeding value (A) from the phenotypic value of the individual (P) depends on h^2. Among traits of conomic importance in meat-producing mammals (table 1), reproductive traits are lowly heritable and, at the opposite, arcass composition traits are highly heritable. Heritability of meat quality traits is generally of low to moderate magnitude hereas heritability of growth rate and efficiency is of the order of 0.30.

- Number of genes

Opinions differ among geneticists as regards the number of genes implied in the variation of quantitative traits : from a w genes (e.g. THODAY and THOMPSON, 1976) to several hundreds of genes (e.g. MATHER and JINKS, 1971). This mber is difficult to estimate experimentally. However, one can calculate the expected number of QTL's affecting a trait of eritability h^2 under restrictive hypotheses (equal effect D and equal gene frequencies p and q at each two-allele QTL). Results e shown in table 2 for various combinations of the above parameters. The number of QTL's with large effects, say D>1, is nited, unless the heritability is high and gene frequencies greatly differ at each locus (i.e. pq=0.10).

In real situations, the size of gene effects as well as gene frequencies are not, of course, the same for each QTL. So, the enetic variation of any trait results from an unknown mixture of occasional major genes (D>1), a number of genes with

Table 1 - Average heritability values of economically important traits in meat-producing mammals

Traits	Usual range of heritability
Reproductive efficiency (litter size, fertility)	0.02 - 0.10
Meat quality traits (e.g. colour, water holding capacity, pH, tenderness)	0.15 - 0.30
Growth traits (average daily gain, feed efficiency, appetite)	0.20 - 0.40
Fat quality traits (e.g. fatty acid composition of pig backfat)	0.30 - 0.50
Body composition traits (lean content, fat content, rib eye area,...)	0.40 - 0.60

Table 2 - Expected numbers of quantitative trait loci (QTL) for different values of heritability and gene frequency (1)

Heritability of the trait	Gene frequency situation (2)	D = difference between the two alternative homozygotes, in phenotypic standard deviation units				
		1/8	1/4	1/2	1	2
0.10	0.10	128	32	8	2.0	0.5
	0.25	51	13	3	0.8	0.2
0.30	0.10	384	96	24	6.0	1.5
	0.25	154	38	10	2.4	0.6
0.50	0.10	640	160	40	10.0	2.5
	0.25	256	64	16	4.0	1.0

(1) It is assumed that all QTL's have 2 alleles (*A* and *a*), with equal effect (D) and equal gene frequencies (p for *A* and q for *a*).
(2) The value reported is the product pq : 0.10 corresponds to very different allele frequencies at each locus (p=0.90, q=0.10), 0.25 corresponds to equal allele frequencies (p=q=0.50).
intermediate effects (0.25<D<1) and many minor genes (D<0.25).

- Major genes

Several genes with large and sometimes very large effects on commercial traits in meat-producing animals have been identified. These include the double muscling gene (*mh*) in cattle (e.g. HANSET and MICHAUX, 1985), the "Booroola" gene affecting ovulation rate and litter size in sheep (e.g. PIPER et al, 1985), the halothane sensitivity gene (Hal^n) responsible for malignant hyperthermia syndrome and pale, soft, exudative (PSE) meat condition in pigs (e.g. OLLIVIER et al, 1975), the "stress-free meat" gene (RN^-) in pigs (LE ROY et al, 1990), and the sex-linked dwarf gene (*dw*) in poultry (review by MERAT, 1986). It is worth noting that two major QTL's (Hal and RN) are involved in the variation of pig meat quality, each of them influencing different parameters of the curve of post mortem fall in muscle pH : the rate of pH fall and pH_1 for Hal and the ultimate pH (pH_u) for RN.

1.2. Genetic polymorphisms

Several methods are available for detecting and describing genetic polymorphisms in the genome of domestic animals. "Classical" polymorphisms which were the only available until recent years are based on visible traits, such as coat colour, polledness, specific tests (e.g. exposure to halothane in pigs), one-dimensional and two-dimensional electrophoresis of blood and milk proteins) and immunological techniques (blood groups, major histocompatibility complex,...).

In the last 10-15 years, the appearance of methodologies allowing to describing genetic variation at the level of DNA itself has been at the origin of several new classes of genetic polymorphisms (see, for instance, SOLLER, 1990).

- Restriction fragment length polymorphisms (RFLP).

This technique basically lies on the use of a group of enzymes (restriction endonucleases), each of which is able to cut DNA molecule at a large number of sites. Each cleavage site is defined by a specific 4 to 8 bp nucleotide sequence (4 to 8 base pairs), and each restriction enzyme is specific to sites having a particular nucleotide sequence . After enzyme digestion, resulting DNA fragments of various length can be separated by gel electrophoresis. As the size of the whole genome is large (about 3×10^9 bp for the haploid mammalian genome), the number of DNA fragments is considerable and a technique was developed in the mid-1970's for identifying a particular fragment, by use of a previously cloned and labelled gene sequence which serves as a probe to locate its homologue on the electrophoresis gel ("Southern blot"). Most RFLP's

far, whether resulting from point mutations or more important changes (deletion, insertion) in the DNA, are diallelic in ure, as found for instance in cattle (FRIES et al, 1989).

- **Variable number of tandem repeats (VNTR) loci : minisatellites and microsatellites**.

In the mid-1980's, polymorphisms consisting of a varying number of a tandemly repeated DNA sequence were found in mans. A number of probes, hybridizing to such VNTR regions, were developed and the electrophoretic banding patterns peared to be unique to different individuals (DNA fingerprinting for individual identification and parentage checking). These NTR loci, containing repeated sequences of 10 or more base pairs, are termed minisatellites and can be extremely lymorphic.

A more recently described class of VNTR loci is based on "microsatellite" sequences consisting of several or many peats of 2 to 4 bp. These microsatellites exhibit site-specific length variation, similar to that shown by minisatellite sequences, d are highly polymorphic. Poly(TG), the most frequent microsatellite motif, appears as 5 to 10 x 10^4 individual islets persed throughout the genome of many species. This number of poly(TG) microsatellites, if they are randomly distributed, uld mean that a microsatellite islet of that type is present every 50 to 100 kb in the genome (kb = 1000 bp). In addition, the dy of microsatellite polymorphisms can be facilitated by the use of polymerase chain reaction (PCR) amplification.

1.3. Associations between QTL's and markers

The observation of a significant association of a quantitative trait with the segregation of alleles at a marker locus dicates either that part of the variation of the trait is due to a pleiotropic effect of the marker gene (the marker is then the TL) or that the marker locus is linked with one segregating locus (or perhaps several loci) controlling part of the variation of e trait. In the latter case, the effect of the marker is due to a statistical association (linkage disequilibrium) between alleles at e marker locus and the QTL : a limitation is that recombination events (crossing-over) between the two loci may reduce the kage disequilibrium and therefore the strength of the association, unless the marker locus and the QTL are very closely ked.

Methods for detecting QTL's through linked markers will not be developed here. A number of methods using population ferences are based on comparisons between marker genotypes for the trait of interest in the F_2 generation of a cross tween populations (breeds or eventually inbred lines). Other methods are based on within-family comparisons between rker genotypes in a particular segregating population. For more details on experimental designs of QTL-marker linkage dies, see SOLLER and GENIZI (1978), BECKMANN and SOLLER (1988), SIMPSON (1989), WELLER et al (1990) and OTZ and OLLIVIER (1992). According to SOLLER (1990), studies based on crosses would be most effective for detecting TL's affecting traits whose value differs to a large extent between populations (e.g. populations differing in susceptibility to a rticular disease or in reproductive traits), while studies based on within-family comparisons in one population would be most ective for detecting QTL's affecting traits showing large within-population genetic variance (e.g. meat content).

A common characteristic of marker-QTL linkage studies is the large size of the design to set up. From theoretical nsiderations, it turns out that several hundreds and more often 1000 to 2000 animals are required to detect QTL's having ects of, say, 0.3-0.5 standard deviation units and that QTL's having effects of less than 0.2 standard deviation units will be y hard to detect, even in very large experiments (more than 5000 animals).

By analogy with the human genetic map, the total map length in domestic mammals is expected to be 30 Morgans (M), e Morgan representing the distance on which on average one crossing-over occurs each time a gamete is formed. Given a sired map distance of 20 cM (cM = centimorgan) between adjacent markers, around 150 markers would be required to tain an evenly distributed genetic map. In fact, much more markers will be probably needed to generate a useful map for eeding purposes. Firstly, there is no a priori information on the location of the markers. Some chromosomal regions will be er-represented in the map and others under-represented. At that point, however, it should be possible to exploit mparative gene mapping data to search for markers whose location is known in other species in order to fill the remaining ps in the map to be completed. Secondly, a given animal will be informative only for the marker loci for which it is terozygous.

1.4. Marker-assisted breeding methods

The question relative to direct selection on specific quantitative trait loci and to indirect selection through linked marker has received attention for more than 25 years (e.g. SMITH, 1967 ; SOLLER, 1978 ; SMITH and WEBB, 1981). However, the erest for this question has been recently renewed with the appearance of DNA-level markers in the 1980's, since this class markers potentially provides a much higher density of genome coverage and shows a higher degree of polymorphism. The ciency of marker-assisted selection as compared to traditional methods of selection on phenotype has been examined on oretical grounds by several authors (e.g. SMITH and SIMPSON, 1986 ; BECKMANN and SOLLER, 1987 ; HANSET, 1989 ; NDE and THOMPSON, 1990).

1.4.1. Marker-assisted selection

In general terms, for a trait of additive genetic variance σ^2_A, genetic gain per unit of time is given by $\Delta G = i\rho\sigma_A/t$ =intensity of selection, ρ = accuracy of selection (correlation between the criterion of selection and the true breeding and t = interval of generation.

Using information on QTL's, directly or most often through markers, may affect each of the 3 above para (OLLIVIER, 1990) :

(1) Accuracy of selection. Markers give a supplementary information which, combined with usual performance allows increases in the accuracy of estimation of breeding values. In individual selection schemes, this may be par useful for traits which cannot be accurately predicted on the live animal (carcass traits).

(2) Interval of generation. Markers may affect time of selection. Information on QTL-markers (e.g. blood markers usually available at birth or in the young age, allowing early selection decisions and a decrease in interval of gen (especially for traits expressed late in life such as reproductive traits). Early screening by means of markers may also reducing the numbers of individuals entering performance test or progeny test procedures, which leads to saving in costs.

(3) Intensity of selection. Selection based on markers can be made independently of sex (as well as of age) instance, allows to evaluate males and to increase intensity of selection for traits expressed only in females (e.g. prolific

In order to assess the interest of taking into account additional information provided by marker loci, consider the case of individual selection on a single trait. The marker information may be summarized by a "molecular score" (see and THOMPSON, 1990) and marker-assisted selection criterion is an index $I = b_1P + b_2M$ with P = individual ph value and M = individual molecular score. The relative efficiency of marker-assisted selection (based on the inc compared to individual selection (based on P alone) is given by $R = \sqrt{(m/h^2) + [(1-m)^2/(1-mh^2)]}$ with h^2 = heritability o and m = proportion of the additive genetic variance which is associated with the marker loci contributing to the m score. Values of R for different values of h^2 and m are given in table 3. In that situation, the advantage of including information in selection is substantial for traits of low heritability if an important fraction of the additive genetic va associated with the markers. However, it must be kept in mind here that most of the QTL's affecting a lowly heritable ch are expected to have small effects (see table 2) and therefore that only QTL-marker linkage experiments of very large enable to detect such QTL's.

Table 3 - Relative efficiency (R) of marker-assisted selection and individual selection (see text)

m	h2			
	0.05	0.10	0.25	0.50
0.25	2.36	1.75	1.26	1.07
0.50	3.20	2.29	1.51	1.17
0.75	3.88	2.75	1.75	1.26
1	4.37	3.16	2.00	1.41

A particular type of marker-assisted selection is that concerning a specific single locus previously detected as major effect on certain quantitative or qualitative traits. In pigs, the halothane sensitivity locus (Hal) belongs to a w linkage group encompassing several blood marker loci (Gpi, H, Pgd, A1BG,...). Some of these "classical" markers h used for reducing the frequency of the halothane sensitivity gene either from examination of within-family segregation and JUNEJA, 1985) or on a population basis in one breed showing strong linkage disequilibria between Hal and m (SELLIER, 1985). Recently, further progress has been achieved for the control of the halothane gene with the disco DNA-level marker relative to the ryanodine receptor (RYR), the calcium release channel of the skeletal muscle sar reticulum. A single point mutation at nucleotide 1843 of the RYR gene has been identified as being correlated probably being causative of, halothane sensitivity in several porcine breeds (FUJII et al, 1991 ; OTSU et al, 1991).

1.4.2. Marker-assisted introgression

Given a resource population identified as containing a favourable QTL allele which one wishes to introduc existing commercial breeding stock, two procedures are available according to that donor and recipient populatio differ greatly or differ greatly in overall economic merit. In the first case, it is possible to create a "composite" popula carry out a breeding programme in this new population. In the second case, it will be better to implement an int

ogramme in order to introduce the desired favourable gene from the donor to the recipient population without appreciably ducing the genetic level of other economically important traits in the latter population.

An introgression programme consists of carrying out a series of backcrosses between the two populations, with the ipient commercial population as the recurrent parent, for reducing to a minimum the contribution of the donor population, er than the desired favourable allele, to the final new population. Use of markers greatly facilitates the introgression since it ows to keep the frequency of the favourable allele at maximum levels (i.e. 0.50) until the end of the backcrossing ocedures. Marker-assisted selection can also be useful by allowing a more rapid fixation of the introgressed gene in the bsequent intercross generations. The most favourable situation is to have the introgressed gene "bracketed" by a pair of arker loci, with a marker haplotype which is unique to the donor population. The primary advantage of a marker haplotype compared to a single marker is that recombination events changing the linkage relationships between QTL and marker eles can be detected.

UTILIZATION OF TRANSGENIC ANIMALS

2.1. Historical background

The ability to insert functional foreign genes into the germ line of animals is one of the major recent advances in biology. e first animals carrying experimentally introduced foreign genetic material (virus SV40) were produced in the mid-1970's. owever, it was the paper published by PALMITER et al (1982) on "giant" transgenic mice (showing, in some cases, a nearly ubled size compared to their non-transgenic littermates) which really attracted the attention of geneticists working on large mals. Following this pioneer work on mice, most gene transfer experiments with farm animals have been concerned with e manipulation of concentration of circulating somatotropin by means of the integration of a number of copies of foreign owth hormone gene into the genome : for reviews, see PURSEL et al (1989), CLARK (1990), HOUDEBINE (1990), WALL et (1990). The first transgenic rabbits, pigs and sheep were produced by the mid-1980's (HAMMER et al, 1985 ; BREM et al, 985).

2.2. Methods for gene transfer

Several methodologies are currently being used to produce transgenic animals (JAENISCH, 1988). In mammalian ecies, the most widely and successfully used method is the microinjection of cloned DNA directly into the male pronucleus a fertilized egg. Infection of embryos at various developmental stages by retroviral vectors can also be used, this method ing probably the only feasible for generating transgenic chickens. A more recently developed technique involves the troduction of genes by DNA transfection or retroviral transduction into embryonic stem (ES) cells, which are capable to lonize the host blactocysts and to contribute to the germ line of the resulting mosaic animal.

Transgenesis is based on fusion genes made of parts from several genes. The transferred genes usually consist of a gulatory element (promoter or enhancer) from one gene fused to the structural DNA sequence of another gene. For stance, the first transgenic pigs (designated mMT-hGH) were obtained from gene constructions composed of mouse etallothionein-I as promoter and human growth hormone gene as structural gene (HAMMER et al, 1985 ; BREM et al, 1985).

2.3. Integration and expression of transgenes

Overall efficiency of transgenesis remains low, as shown in table 4 (WALL et al, 1990) : the proportion of transferred icroinjected eggs which result in an individual expressing the transgene is 2% in mice and appears to be 5-10 times lower in gs and sheep. Prenatal mortality is a significant contributor to the inefficiency of transgenesis in pigs and sheep as less than % of the microinjected eggs develop to term. However, in pigs as well as in mice, transgenes are expressed in transgenic dividuals at a rate of 60%. A general feature of producing transgenic animals by DNA microinjection is the highly variable mber of transgene copies which become integrated at a single random site of the host genome. In addition,the amount of ne product seems to be incorrelated with the number of inserted transgene copies. So, the level of expression of a rticular transgene is unpredictable and each transgenic animal is essentially unique.

2.4. Transmission of transgenes

A transgene (*T*) is integrated in one of the host chromosomes to give an hemizygous (*TO*) transgenic individual. The neral rule is that the transgene is transmitted to offspring of the transgenic founder by ordinary Mendelian inheritance (i.e. to bout 50% of offspring). However, abnormal transmission patterns have been observed. As reported by Pursel et al (1990) in gs, a proportion of transgenic boars failed to transmit the transgene to their progeny and were probably mosaics, with tegration only in somatic cells. Mosaicism in the germ line was probably present in a boar who transmitted the transgene to hly 1 of 33 offspring.

Table 4 - Efficiency of transgene integration in three mammalian species (according to WALL et al, 1990)

Item	Species		
	Mouse	Pig	Sheep
Size of data set (*)	>100	70	13
Offspring per injected egg transferred	25%	8%	8%
Transgenics per offspring	10%	8%	6%
Expressors per transgenic	60%	62%	33%
Expressing transgenic per injected egg transferred	2%	0.3%	0.2%

(*) Number of transgenic animals upon which percentages are based.

2.5 Performance of transgenic GH pigs and sheep

In contrast to the observation of a considerably increased growth rate in transgenic mice which express foreign genes, transgenic GH pigs generally exhibit the same daily gain as control pigs (review by PURSEL et al, 1990). efficiency and carcass leanness are markedly improved in transgenics, but the continuous "over-expression" of GH res serious health problems (lameness, gastric ulcers,...) and in impaired reproductive capacity (anoestrus in gilts, lack of li boars). The same pattern of effects was reported in transgenic GH sheep by WARD et al (1990).

2.6. Use of transgenes for livestock improvement

As pointed out by SMITH et al ((1987) and ELSEN (1988), a gene transfert operation conducted for improv particular target trait in farms animals comprises several steps :

- identification of candidate genes
- choice of the most relevant gene for transfer,
- clonage of the gene and development of the gene construction used for transfer,
- production of transgenics,
- screening of the individuals carrying and expressing the transgene,
- evaluation of the merit of each transgenic individual for the target trait and also for all other traits of ec importance,
- testing the transmission of the transgene to offspring,
- development of a transgenic stock from the founder(s) of highest interest,
- dissemination of transgenic breeding animals to commercial farms.

As a general rule, development of transgenics should take place within current nucleus breeding stocks in order to a genetic lag which would ensue if stocks of lower original economic merit were used.

2.7 Other possible use of transgenes

Gene transfer operations in farm animals may be developed to produce novel products, e.g. molecules of value, or to induce compositional changes in traditional animal products such as milk (MERCIER et al, 1986 ; MUYSS VERRINDER GIBBINS, 1989).

3 - SOME OTHER APPLICATIONS OF MOLECULAR GENETICS

A list of other applications of recombinant DNA techniques in the field of animal production is given below.

3.1. Manipulation of sex ratio

Available methods for altering the normal mammalian sex ratio were recently reviewed by Mc EVOY (1992). specific DNA probes in cattle (e.g. LEONARD et al, 1987) and sheep allows to sexing individual embryos in vitro transplantation.

3.2. Genetically engineered vaccines

With the advent of DNA manipulation techniques, a new generation of veterinary vaccines has appeared, as by AYNAUD (1991). Possibility to make distinction between vaccinated and infected animals is one of the major adva these new vaccines.

3.3. Production of "recombinant" molecules for administration to animals

In that area, exogenous administration of bovine somatotropin (bST) or porcine somatotropin (pST) is a w example. In the first attempts to investigate the effects of daily injections of pST on pig growth performance, purified pituitary extracts were used. In the 1980's, progress in genetic engineering allowed that manipulated micro produce large quantities of highly purified recombinant growth hormone and it was shown that recombinant pST has

ects as native pituitary pST (EVOCK et al, 1988). The effects of exogenous pST administration to growing-finishing pigs re recently reviewed by BONNEAU (1991). However, the legal authorization for the use of pST by pig industry remains certain.

3.4. Labelling of animal products

The probable appearance of a very large number of DNA-level polymorphic markers in farm animals leads some ople to think that in the future it could be possible to "patent" the origin of animal products, e.g. meat from a particular ecies or even from a particular breed.

ONCLUSION

There is no doubt that the considerable advances in molecular genetics and DNA manipulation offer new opportunities applications in the area of genetic improvement of farm animals. However, too optimistic views on the immediate potential these new methodologies should be avoided and, as pointed out by KENNEDY et al (1990) among others, debates on olecular versus quantitative genetics are essentially meaningless.

Traditional breeding methods, though lying on fairly simplistic genetic models, have been, and still are, a powerful tool generating genetic changes in many traits, particularly in traits showing moderate or high heritability (growth efficiency and rcass composition). Many geneticists agree for considering that selection based on DNA-level markers should not be seen an alternative to current methods of selection on phenotype. The true question is where and how information on markers be integrated into the quantitative framework of traditional breeding programmes. The best theoretical prospects for lating marker-assisted selection schemes concern lowly heritable traits. In that case, the problem however remains to be e to detect a sufficient number of QTL's with appreciable effects in order to have a noticeable proportion of the additive netic variance which is associated with the markers. One can think that in the short term marker-assisted selection will be st efficient for "point" actions dealing with a few major QTL's which are already identified for most of them. This approach s been examplified in the last few years by the discovery of DNA-level blood markers for the halothane gene in pigs and sein genes in dairy animals.

As for the gene transfer technology, results found so far on the integration of growth-related transgenes in pigs and eep are rather disappointing from an overall point of view, due to highly unfavourable correlated effects on health and tility. Prospects for transgenesis are perhaps of greater promise if the purpose is to modify composition and/or quality of mal products. However, it is felt that muscle and meat are less suitable targets than milk for this type of genetic engineering. , it is not, at this stage, obvious that genetically modified animals will play a role, in the near future, in meat-producing ecies.

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