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Zootechnical and genetic potential in crossbreeding experiments and breed comparisons

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SUMMARY - Published works on rabbit genetics involving crossbreeding and breed comparisons are reviewed. Construction and analysis of crossbreeding experiments are discussed with special reference to direct, maternal heterosis as well as recombination effects. Two main models of crossbreeding analysis are proposed from the available literature.
Key words: Rabbit genetics, crossbreeding, heterosis, recombination effects, breed comparisons.

RESUME - "Potentiel zootechnique et génétique dans le cadre d'essais de croisement, et comparaison de races". Les travaux publiés sur la génétique du lapin dans le cadre de croisements et comparaisons raciales sont révisés. La construction et l'analyse d'expériences de croisement sont discutées, avec une référence particulière aux effets génétiques d'hétérosis direct, maternel, ainsi qu'à ceux de recombinaison. Deux modèles principaux d'analyse de plans de croisement sont proposés compte tenu de la bibliographie.
***Mots-clés :** Génétique du lapin, croisement, hétérosis, effets de recombinaison, comparaison de races.*

Introduction

In animal breeding, crossbreeding allows the exploitation of breed qualities from both the genetic and the biological standpoint. It is also a tool for breed discrimination and for the analysis of genetic variability. Works presented here suggest that we have objective criteria, scientifically established to characterize reproductive and growth aptitudes in unfavorable environments.

The aim of this work is to show the role of a crossbreeding experiment, to define the reasoning and its implementation as well as to expose its interpretation.

A crossbreeding experiment. A step within a process

Several articles (Rouvier, 1980;. Matheron, 1982; Masoero, 1982; Matheron and Poujardieu, 1984; Rochambeau, 1988) report most of the published crossbreeding experiments in rabbits. In general, a crossbreeding experiment is a step within a process of knowledge acquisition. We shall limit ourselves to the knowledge needed in a plan for rabbit breeding. A crossbreeding experiment can help in the choice of breeds to be improved and in the definition of breed utilization.

BREED CHOICE

Works by Brun and Rouvier (1984, 1988) illustrate the utilization of crossbreeding experiments in breed choice. From 1961, after a control of field performance, we know the management conditions and breed availabilities (Rouvier *et al.*, 1973). In 1970, public financed research defined a national plan of rabbit improvement: the commercial product shall come from a prolific crossbred female mated with a meat type male. I.N.R.A. takes the task of amelioration of the female parent.

From the known breeds, which ones should be chosen in order to be selected? and, for what traits? For each trait of zootechnical interest we have to estimate the additive genetic variability, the sole characteristics used in within breed selection. For joint characters it is also necessary to evaluate stable favorable associations (complementarity). The tool came after setting up a complete factorial design of three breeds mated with each other and a common testing male mated with the nine genetic types from the first cross.

Results from this experiment, modified by selection, shall be evaluated in standard farms: rabbits are raised in cages inside a rabbitry, with controlled environment, organized management; often having rabbits as their main activity. Field station monitoring seemed the rational approach.

DEFINITION OF STRAIN UTILIZATION

Within a given farm context, several genetic types can be used. How to utilize them from a scientific approach was the work reported by Ouhayoun (1977). Knowledge about the estimation of specific combining ability became as important as the estimation of general combining ability.

Within these types of experiments, the most often in literature, tools are as varied as the objectives are; these go from the complete diallel, where the objective is a complete genetic matrix, to the realization of several combinations where heterosis is the main goal. Since knowledge of the specific combining ability is important, the choice of the environment where the experiment is developed is a sensitive task; even more than for the preceding situation it should correspond to the environment where results are evaluated.

In the following examples (Ouhayoun, 1977) results are evaluated at rational exploitations; a research station is suitable in this case. Sometimes results should be evaluated at an unfavorable environment, such as that of the Guadalupean rabbit production (Matheron and Dolet, 1986), where a crossbred experiment was impossible.

Strain A 1077, selected at I.N.R.A. shows an adaptation ability to unfavorable thermal hygrometric conditions (30° C and 80% relative humitidy, Poujardieu and Matheron, 1984). A cross of this strain with autochthonous animals allows the improvement of the Guadalupean rabbits. The retained selection came after performing the crossbreeding at the Centre de Recherches Antilles Guyane Station and later to diffuse breeding stock to the producing farms where their productions were monitored thanks to the performance control I.N.R.A.-I.T.A.V.I. This device assures the necessary fixation of the action: at the farm the zootechnical amelioration is regarded and the animal movements measured, in station the knowledge of prolificacy of grand-parent stocks allows the definition of a diffusion policy.

This last example is that of the introduction of an exotic strain. It shows the interest of thermal tolerance studies which, other than for the physiological knowledge that might be involved, help in the choice from the available strains of those susceptible to be adapted.

The aim of a crossbreeding experiment is the acquisition of knowledge which, after their evaluation, improves the local rabbit productions in their technical, economical and social aspects. There is a categorical imperative of success. A fair appreciation of the permeability to the innovation from those who evaluate the results is a condition for the choice of a realistic objective. As any experiment, an experiment of crossbreeding is a way of testing a hypothesis formulated in a dialogue between knowledge and assignable resources.

How to construct a crossbreeding experiment

The term crossbreeding experiment involves a series of experimental designs. Rather than to describe them, we will develop here a didactical tool adapted to any case. It responds to the decomposition of the mean value of a genotype in their genetic effects (Dickerson, 1969; Rouvier and Brun, 1990).

The first intellectual landmark comes after assigning a trait to an individual. A weight at a given age or the growth rate is a trait of the individual. The attribution to the progeny of the litter size of the mother is often argued. To consider litter size as a dam trait is analogical to ignore the existence of a sire genetic effect on the litter that he fathers (Matheron, 1982). At least in the case of inbred individuals this effect certainly exists (Chai, 1969). The only coherent situation is to assign litter size to the progeny.

Under an assumption of no epistasis (Eisen, 1983), the trait average value for a genotype is the addition of average direct genetic effects, maternal and grand maternal... direct heterosis if the individual is crossbred, maternal heterosis if the dam is crossbred, and if there is epistasis recombination effects if the individual comes from at least a crossbred parental. Table 1 shows the decomposition for different types and crosses.

The direct genetic effect is the individual gene contribution to the trait value. This will be expressed as the average of the direct genetic effects of the parental

strains. The maternal and grand maternal genetic indirect effects are an environmental effect for the individual. They are the contribution to the trait value of the individual due to the environmental effect of the dam genes or grand dam genes. These are statistical contributions; they are defined as a translation considering the experimental conditions under which they were obtained.

The theoretical expressions of the averages are utilized both to design and to analyze a crossbreeding experiment. Once the comparable strains are chosen, the design of a crossbreeding experiment corresponds to the simulation of several devices and the confrontation of them to the objective. The estimator precision is also an element of decision (Cunningham and Connolly, 1989; Sölkner and James, 1989).

How to analyze a crossbreeding experiment

The aim of the analysis is to obtain the estimates of the relevant genetic effects with a maximum precision. Very often, once an experiment has been realized, the parasite effects that we want to eliminate are joined to the genetic effects. The way they are distributed in the genetic effects is a choice criteria among the two types of models normally utilized when analyzing a crossbreeding experiment.

Within the first model we describe the estimable genetic effects as fixed. Sellier (1982) has discussed several models of this type according to the objectives and the experimental tools. In the case when heterosis and recombination effects are the main goal, Bosch (1987) has proposed a type of model based upon Hill's (1982) decomposition of the value of the mean. Each line or two line cross is decomposed in their genetic effects, namely: α, δ, $\alpha\alpha$, $\alpha\delta$ and $\delta\delta$; which corresponds to additivity, dominance and the first order interactions between these two: additive by additive, additive by dominance and dominance by dominance interactions as first suggested by Cockerham (1954).

The second type of model is expressed no longer in function of the genetic effects but under the basis of genetic type effects. The analysis is decomposed in two phases (Brun and Rouvier, 1984): estimation of average genotypic values and estimation of genetic effects. The genetic parameters are estimated by the estimable functions, linear combinations with constant coefficients of average estimated genotypic values, where summation of coefficients is zero (Rouvier and Brun, 1990). The choice of any function is dictated by means of isolating a genetic effect. The variance of the estimator of the genetic effect is obtained by the quadratic form constructed with the coefficient vector that defines the linear combination and the covariance matrix of the estimates. The comparison to zero of an estimated genetic effect is performed after a Student-Fisher t statistic.

A one step calculation can be used by GLM procedure from SAS (1986) in order to get the estimates of the functions giving the crossbreeding genetic parameters (genetic effects) and the genotypic values as well as to test their significance.

Conceptually, both models applied to the same experiment conduct to the same genetic hypotheses. The first model can be deduced from the second in its genetic elements by replacing the levels of the descriptive breed effects by their theoretical expressions (Tables 1 and 2). Accordingly, maternal main effects and maternal second order interactions can be deduced from table 2 by assigning to each individual the corresponding coefficients of their mother's direct main genetic effects and direct second order interactions (table 3).

When working with direct effects only, heterosis of line A with line B, AB is:

$$AB = \overline{F_1} - (P_A + P_B)/2$$

Recombination effects ab are:

$$ab = \overline{F_2} - \overline{F_1}/2 - (P_A + P_B)/4$$

With Hill's parametrization:

$$AB = 2\delta - \alpha\alpha$$

$$ab = -\alpha\alpha/2 - \delta\delta$$

$$AB/2 - ab = \delta + \delta\delta$$

The better F_1 perform over P_A and P_B, the bigger AB is, which in turn can be due to either δ or $\alpha\alpha$, or both. If δ is big and positive we then have a case of strict dominance. In this case difference between heterosis and recombination effects should be big since it estimates δ and $\delta\delta$ together. If $\alpha\alpha$ is big and negative, new second order interactions have arisen from genes of line A and line B. In order to discern between these two cases, for $\alpha\alpha$ being big and negative, backcrosses should perform worse than expected from main additive effects, since their expected values carry 1/4 $\alpha\alpha$ (Bosch, 1987).

The existence of important $\alpha\alpha$ second order interactions can help in the development of synthetic lines from crossbreeds, since $\alpha\alpha$ can be fixed in the new line.

Another tool to exploit favorable interactions is to look at quadratic forms of $\alpha\alpha$:

$$AA = \Sigma\,(\alpha\alpha^2_{ij})_k$$

where segregation is over all relevant loci (ij), and assuming summation over all relevant pairs of loci (k) differing pair-wise in the two original lines (Bosch, 1987).

Means to evaluate AA and other quadratic forms of second order interactions are described in that work.

Conclusions

Several strategies can be used to analyze and evaluate the magnitude of heterosis and recombination effects, as well as their meaning in terms of main effects and second order interactions. These tools can help in the design of complex mating programs, leading to the improvement of the overall efficiency of the production scheme.

The capacity to estimate the different parameters will depend upon the availability of both physical and analytical resources since several crosses should be tested and evaluated in contemporary basis.

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TABLE 1. Direct effects, maternal and grand maternal effects, heterosis, recombination effects.

Mating	Direct effects	Direct heterosis	Recombination effects	Maternal effects	Maternal heterosis
P_A	A			A	
P_B	B			B	
A x B	(A + B) / 2	AB		B	
B x A	(A + B) / 2	AB		A	
$(A \times B)^2$	(A + B) / 2	AB/2	ab	(A + B) / 2	AB
A x (A x B)	(3A + B) / 4	AB/2	ab/2	(A + B) / 2	AB
B x (A x B)	(A + 3B) / 4	AB/2	ab/2	(A + B) / 2	AB

Where AB is the heterosis of A with B, and ab is the recombination effect of A with B.
According to Dickerson (1969).

TABLE 2. Hill's (1982) decomposition of line and crossline average values into main genetic effects and second order interactions.

	α	δ	αα	αδ	δδ
P_A	1	-1	1	-1	1
P_B	-1	-1	1	1	1
A x B	0	1	0	0	1
B x A	0	1	0	0	1
$(A \times B)^2$	0	0	0	0	0
A x (A x B)	1/2	0	1/4	0	0
B x (A x B)	-1/2	0	1/4	0	0

TABLE 3. Application of Hill's (1982) decomposition of line and crossline average values into maternal main effects and maternal second order interactions.

	α	δ	αα	αδ	δδ
P_A	1	-1	1	-1	1
P_B	-1	-1	1	1	1
A x B	-1	-1	1	1	1
B x A	1	-1	1	-1	1
$(A \times B)^2$	0	1	0	0	1
A x (A x B)	0	1	0	0	1
B x (A x B)	0	1	0	0	1