GENETIC ANALYSIS OF SOME PRODUCTIVE TRAITS IN MEAT RABBIT. I.- A MODEL OF DECOMPOSITION OF PHENOTYPIC VARIANCE INTO DIRECT, MATERNAL AND ANCESTRAL COMPONENTS.

Análisis genético de caracteres productivos en el conejo de carne. I.- Modelo de descomposición de la varianza fenotípica en componentes directos, maternales y ancestrales.

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1. INTRODUCTION.

In certain traits dam contributes strongly to the phenotypic value of her products not because of her gene transmission but due to her environmental effects on them; for instance, weaning weight greatly depends on maternal lactation. This component, environmental for the products, can have a genetic and an environmental fraction for the dam. The latter could go on decomposing into fractions attributed to grand-maternal, great-grand-maternal... genotypes and environments. So the phenotypic value of each trait could be divided into several fractions: the effect of the individual's genotype (direct genetic effect) and of the non-maternal environment (direct environmental effect); maternal genetic and environmental effects; grand-maternal genetic and environmental effects, etc.

The estimation of these effects is extremely difficult; FOULLEY and LEFORT (1978) reviewed different methods of estimation. CUNDIFF (1972), MATHERON (1973), VISSAC (1979), WILLHAM (1980) and ROBISON (1981) made reviews about estimation and biological interpretation of maternal effects.

VAN VLECK (1976) has generalized the method of selection indexes including maternal, grand-maternal, great-grand-maternal, etc. genetic effects for each trait. Nevertheless, the use of maternal effects in selection does not seem possible as for the present the estimates, made by different methods, are not trustworthy.

By using special designs that increase the types of relationship is possible to carry out estimates of direct, maternal and ancestral components and the relations among them by least squares methods (EISEN 1967). These designs are incompatible with the normal course of a selection process and taking into account the small accuracy of the estimates the interruption of the process is not probably justified. Nevertheless, attributing the traits to dams and to their products separately and making diverse analysis (ANOVA, regressions) several types of relationship can be related without altering the selection process at all.

Iteration leads occasionally to contradictions but gives complementary information to that supplied by standard error or confidence limits. The methods for estimating maternal effects are little accurate but by repeating the analysis with different data and examining the consistency of parameters it can be possible to reach to some conclusion about the relative importance of the effects and their relations.

In this work a generalization of KEMPTHORNE's formula of covariance between relatives (1957) will be made including in the partition of the variance maternal and ancestral effects. This formula, in a simplified form, will be applied to the different types of relationship obtained on interpreting ANOVA and regression analysis made attributing data to dams and to their products separately. Possibilities of estimation of effects and the relations among them will be discussed from the genetic interpretation of these analysis.

2. DECOMPOSITION OF THE PHENOTYPIC VALUE.

For developing the general formula of covariance among relatives WILLHAM's model (1972) will be used as it is best suited to our purposes. WILLHAM's notation is a little annoying and it will be substituted for another one in which sub-indexes will indicate the generations to which the effect is referred.

\[ P_x = \sum_{j=0}^{J} \left( G_{x_j} + E_{x_j} \right) \]

where \( x_0 \) is the individual, \( x_1 \) the mother, \( x_2 \) the grand-mother, etc. \( P_x \) is the phenotype of \( x \), \( G_{x_0} \) and \( E_{x_0} \) the direct genetic and environmental effects \( G_{x_1} \) and \( E_{x_1} \) the maternal effects, \( G_{x_2} \) and \( E_{x_2} \) the grand-maternal effects, etc. The last environmental effect \( E_{x_j} \) contains a residue that could go on decomposing into its ancestral \( J+1 \), \( J+2 \), etc. effects.

Genetic effects can be decomposed into their additive, dominant and epistatic components.

\[ P_x = \sum_{t=0}^{n} \sum_{s=0}^{n} \sum_{j=0}^{J} A_t x_j D_s + \sum_{j=0}^{J} E_{x_j} \]

Assuming that genetic and environmental effects are independent, the covariance between two relatives \( x \) and \( y \) will be:

\[ \text{cov} \left( P_x, P_y \right) = \sum_{i,j=0}^{n} \sum_{t,s=0}^{n} 2^t x_i y_j u_i^t x_j y_j \sigma_i^2 D_i A_j D_s + \sum_{i,j=0}^{n} a_{ij} \sigma_i^2 E_i E_j \]

where \( r_{x_i y_j} \) and \( u_{x_i y_j} \) are respectively the coefficients of relationship and identity between maternal ancestor \( i \) of individual \( x \) and \( j \) of individual \( y \). It is understood that when \( i = j \) the term \( \sigma_i^2 \) is a variance, while in the other cases is a covariance. The coefficient \( a_{ij} \), whose possible values are 0 and 1, indicates presence or absence of the covariance. Its value is 1 when \( x_i \) and \( y_j \) are referred to the same individual, in the other cases environmental effects are supposedly independent (for instance, the term \( \sigma E_1 E_0 \) exists when "y" is the mother of "x", as then \( x_i \) and \( y_0 \) are the same individual: \( x \) mother; in that case \( a_{10} = 1 \).
A simplified case that will be used later on is developed:
\[
\text{cov}(x',y') = 2 r_{x_0y_0} \sigma^2_{A_0} + 2 r_{x_1y_1} \sigma^2_{A_1} + 2 r_{x_2y_2} \sigma^2_{A_2} + 2(r_{x_0y_1} + r_{x_1y_0}) \sigma_{A_0A_1} + 2(r_{x_0y_2} + r_{x_2y_0}) \sigma_{A_0A_2} + 2(r_{x_1y_2} + r_{x_2y_1}) \sigma_{A_1A_2} + \alpha_{00} \sigma^2_E + \alpha_{1} \sigma^2_{E_1} + a_{2} \sigma^2_{E_2} + (\alpha_{01} + \alpha_{10}) \sigma^2_{E_0E_1} + (\alpha_{02} + \alpha_{20}) \sigma^2_{E_0E_2} + (\alpha_{12} + \alpha_{21}) \sigma^2_{E_1E_2}
\]

it is a strictly additive model in which only direct, maternal and grand-maternal effects are considered.

3. INTERPRETATION OF THE STATISTICAL PARAMETERS.

From an operative point of view each trait can be assigned to dams or to their products (to individual or to its mother). For instance individual weaning weight can be considered as a mother's data and on making the genetic analysis it will be necessary to rearrange data according to a hierarchal organization sires-dams of the dams.

Attributing data to the products the components of variance obtained by ANOVA have the following interpretation:

\[
\sigma^2_S = \text{cov}_{HS} \quad \sigma^2_D = \text{cov}_{FS} - \text{cov}_{HS}
\]

were HS means "half-sibs", FS "full-sibs", S "sire" and D "dam".

Attributing traits to dams:

\[
\sigma^2_S = \text{cov}(\text{offspring of half-sisters}) \quad \sigma^2_D = \text{cov}(\text{offspring of full-sisters}) - \text{cov}(\text{offspring of half sisters})
\]

In the case of intra-sire regression of the products mean on dam, being the traits attributed to the products, the numerator of the coefficient of regression is the covariance mother-daughter but when attributed to dams there are two possibilities Mother-daughter and aunt-niece as both mother and aunt's values may be attributed to the grand-mother. Average litter size being from 4 to 6 the second possibility is much higher.

In sire-offspring regressions traits can only be attributed to the products, as maternal effects are transmitted to daughter. The numerator of the coefficient of regression is the covariance between sire and offspring.

As for repeatability each individual is a repetition of dam's traits and for this reason can be considered as a parameter of traits attributed to dams. Repeatability is the sum of sire and dam intra-class-correlation attributing traits to their products.

\[
RE = \frac{\text{cov}_{FS}}{\sigma_p^2} - \frac{\text{cov}_{HS}}{\sigma_p^2} + \frac{\text{cov}_{HS}}{\sigma_p^2} = t_{D}(\text{product}^2) + t_{S}(\text{products})
\]

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It is a parameter linked to the previous ones and does not give new information but it serves to calibrate the importance of systematic effects.

Applying the model of maternal effects to the relationships just mentioned the following Table is obtained:

Table: Components of the variance of the genetic parameters in an additive model with direct, maternal and grand-maternal effects. Data attributed to dams and to their products.

<table>
<thead>
<tr>
<th></th>
<th>$h_0^2$</th>
<th>$h_1^2$</th>
<th>$h_{01}^2$</th>
<th>$h_2^2$</th>
<th>$h_{02}^2$</th>
<th>$h_{12}^2$</th>
<th>$e_1^2$</th>
<th>$e_{01}^2$</th>
<th>$e_2^2$</th>
<th>$e_{12}^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>RE</strong></td>
<td>1/2</td>
<td>1</td>
<td>1</td>
<td>1/2</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>DAM</strong></td>
<td></td>
<td>$1/16$</td>
<td>$1/4$</td>
<td>$1/4$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>RIP</strong></td>
<td></td>
<td>$1/4$</td>
<td>$1/2$</td>
<td>$3/4$</td>
<td>$1/2$</td>
<td>$5/8$</td>
<td>$5/4$</td>
<td>1</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

|          |         | $1/4$   | $1/4$     | $1/1$   | $1/2$     | $1/2$     | $5/8$  | $5/4$     |        |          |
| **PROD** |         |         |           |         |           |           |        |           |        |          |

|          |         |         |           |         |           |           |        |           |        |          |

|          |         |         |           |         |           |           |        |           |        |          |

$\frac{\sigma^2}{A_i} \quad ; \quad \frac{\sigma^2}{E_i} \quad ; \quad \frac{\sigma^2}{A_i A_j} \quad ; \quad \frac{\sigma^2}{E_i E_j}$

$t_s$: sire intra-class correlation, $t_D$: dam intra-class correlation, RIP: intra-sire regression, RP: regression on sire, RE: repeatability.

4. ESTIMATION OF THE EFFECTS AND THEIR RELATIONS.

The component of the variance due to direct genetic effect would be estimated for $4 \times t_s$ (products). This is the usual way of estimating the heritability.

It is not possible to separate maternal genetic effects from the component $h_{01}^2$. Using sire regression the term $1/8 h_{02}^2$ could be dismissed and $h_{01}^2$ and $h_{11}^2$ tried to be determined; but the consistency of the parameter $RP$...
would have to be proved because it is usually estimated from a very small number of sires and is more attached to random variations than other parameters.

Maternal environmental effects component can be estimated for $t_D$ (products) - $t_D$ (dams) - 3 x $t_S$ (dams).

It is not possible to separate the components of grand-maternal effects, but the difference between $t_D$ and $t_S$ gives, all in all, an idea of this effect.

The difference between RIP (products) and RIP (dams) + $t_S$ (products) gives a notion of the value and sign of the direct and maternal components of variance: $1/2 h^2 + e^2$.

The resolution of the system of equations that can be established, dismissing certain components, has two main objections: the first is that it is not possible to fix the estimation error and the second deals with the consistency of the estimation of the statistical parameters. On dismissing a component the estimation of the other ones is subjected to error, the higher the bigger was the value of the dismissed component. In the other hand it is possible that a statistical parameter has very different values in successive estimations, what may lead to a great variability of estimates proceeding from a system of equations in which this parameter is considered.

In this work it is advisable to use for the estimation parameters whose values have been very similar in different estimates. With this method the normal course of the usual program of selection is not altered. Rearranging data and operating in several ways it is possible to deepen in the knowledge of the genetic determination of the studied traits.

**SUMMARY**

A generalization of Kempthorne's formula of covariance between relatives including maternal and ancestral effects both genetic and environmental in the partition of variance, is proposed in this work. Its main purpose is to increase the types of relationship in data analysis by attributing traits to dams and to their products separately and by the realization of analysis of variance and regressions. This method does not interrupt the normal course of a selection process as it increases the types of relationship without altering the hierarchal plan of mating. Finally, the possibilities of estimating direct, maternal and ancestral effects as much as their relations from the genetic interpretation of the above mentioned analysis are studied.

**RESUMEN**

En este trabajo se generaliza la fórmula de Kempthorne de varianza entre parientes, incluyendo en la partición de la varianza los efectos maternos y ancestrales. Se propone el aumentar los tipos de parentesco en los análisis de datos mediante la atribución por separado de los caracteres a las madres y a los productos, y la realización de análisis de la varianza y regresiones. Este método no interrumpe el curso normal de un proceso de selección, pues aumenta los tipos de parentesco sin modificar el plan jerárquico de apareamientos. Finalmente se examinan las posibilidades de estimación de efectos directos, maternales y de abuela, y de sus relaciones, a partir de la interpretación genética resultante de los análisis propuestos.
5. REFERENCES


