



FEED-A-GENE

Adapting the feed, the animal and the feeding techniques to improve the efficiency and sustainability of monogastric livestock production systems

Deliverable D5.3

New methodologies to account for repeated measurements, social effects, and variability in performance in genetic evaluations

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1. Summary

Objectives

The general objective of this task was to develop statistical models and procedures as well as new software for selection on feed efficiency and robustness.

Specifically we have worked on three main topics of research:

- 1. Improvement of models and procedures for selection on feed efficiency taking into account the characteristics and structure of the data
- 2. Definition of models and procedures to account for indirect genetic (IGE) and environmental effects (i.e., social interaction effects) on growth and feed efficiency
- 3. Selection for the individual's environmental sensitivity (robustness) and interaction between the genotype and feeding regimen

Rationale

Pig and rabbit data originating from task 5.1 and task 5.2 were used to implement the proposed models and procedures in task 5.3, which were developed following a frequentist or a Bayesian approach. The implementation of the statistical methodologies were developed from existing software and their details are available in the published papers. Models were compared in terms of goodness of fit, predictive ability, and response to selection on real and simulated data. In addition, a freely available software module was developed that allows multiple-trait analyses.

Regarding the first topic of research, we have developed and implemented the structured antedependence model (SAD) for the analysis of longitudinal records of feed conversion ratio (FCR). This model fits the covariance structure of the data with few parameters better than other models and provides unbiased estimates of the correlation between distant measurements of the trait. A selection criterion combining the weekly breeding values using the eigen-decomposition of the genetic covariance matrix was proposed to summarize the individual estimated breeding value (EBV) trajectory into a reduced number of parameters for practical applications to selection. We have also assessed the impact of missing records of body weight on the prediction of breeding values and estimation of genetic parameters of FCR and have proposed a procedure to impute them. The potential of genomic information to improve the accuracy of breeding value predictions for residual feed intake, applying single step genomic approaches to the random regression and SAD models was also assessed. We proposed a procedure to estimate breeding values and genetic and environmental parameters of feed efficiency from group records of feed intake and individual records of body weight gain and metabolic





weight at fattening. In this procedure, feed efficiency is defined as a conditional trait derived from elements of genetic and environmental covariance matrices. These measurements of feed efficiency are genetically and phenotypically uncorrelated with production traits. Thus, selection for this trait does not lead to unfavourable correlated responses on production traits.

Models and procedures to account for the genetic and environmental social interaction effects (also known as indirect genetic effects, IGE) on growth and feed efficiency were proposed. A specific degree of interaction between each pair of animals sharing the same pen/cage was defined by the correlation between each pair of pen/cage mates for different feeding behaviour variables obtained from electronic feeder data. This information alleviates collinearity and improves the model performance and led to a more accurate genetic evaluation of traits affected by IGE. We also have investigated how IGEs vary over time implementing a structured antedependence (SAD) model that includes IGEs. We have evaluated, by simulation, the response to selection on longitudinal average daily gain (ADG) using different selection strategies. We have also estimated the effect of the interaction between the genotype and feeding regimen and we have elucidated the origin of such an interaction.

Finally, we have developed a software module for genetic analysis of multiple-traits heteroscedastic models. This software allows to estimate the magnitude of animal genetic sensitivity to express a specific trait in different environments or for different traits. Thus, it allows knowing the genetic determinism of a definition of global robustness as the genetic correlation between the sensitivities of different traits to environmental variations. The software is implemented in ASRemI-4.

Teams involved

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Species and production systems considered:

The results of this deliverable can be applied to any farm animal species. Tests and demonstrations were run on pig and rabbit datasets.





2. Introduction

The general objective of this task was to develop and implement models and software for direct selection for feed efficiency and robustness, which take into account the characteristics and structure of the data coming from different species and the existence of several factors generating genetic variability that can be used to improve this important trait.

Specifically, we have worked on the following topics:

1. Improvement of models and procedures for selection on feed efficiency taking into account the characteristics and structure of the data

With the development of electronic feeders, it is possible to individually record feed intake throughout the production period in species such as pigs. This information can lead to more accurate estimates of genetic parameters and breeding values than using single measurements. However, to analyze longitudinal data it is necessary to implement appropriate models with few parameters that account for the covariance structure of the repeated records. A common measurement of feed efficiency is feed conversion ratio (FCR), which corresponds to the ratio of feed intake (FI) to body weight (BW) gain. The analysis of individual patterns of FCR requires the availability of longitudinal records of the two traits. However, these two traits are not usually measured at the same time or with the same frequency. While there are daily records of FI obtained from the electronic feeders, BW is measured weekly or even monthly. Thus, there can be missing records of BW for substantial parts of the growing period. This can have an impact on the estimation of genetic parameters of FCR. In addition, a method for imputation of missing BW that minimizes this impact must be found.

Electronic feeders are expensive equipment that are not available for all the species hitherto. Measurement of FI at the group level is feasible and cheaper than individual recording but the use of this kind of information for selection requires appropriate models and definitions of feed efficiency.

With current definitions of feed efficiency such as residual feed intake (RFI), there is no phenotypic correlation between residuals and the explanatory variables representing the animal's requirements, but this does not guaranty having null genetic correlations. In fact, unfavorable genetic response on growth has been observed after selection for RFI calculated from phenotypic regressions (Gilbert et al., 2007; Cai et al., 2008). To avoid these undesired





effects, it is necessary to base the correction of FI not on the phenotypic regression, but on the genetic regression of FI on production traits, as proposed by Kennedy et al. (1993), who defined this as "restricted residual feed intake" (RRFI), because of its equivalence to a restricted selection index in which production traits are held constant. This definition of RRFI guarantees null genetic correlation with performance traits, and thus null correlated responses among them. Implementation of this or of similar definitions of feed efficiency has been previously performed using multiple-trait models for individual records (Strathe et al., 2014; Shirali et al., 2018) but not for records for group-housed animals.

2. Definition of models and procedures to account for indirect genetic (IGE) and environmental effects (i.e., social interaction effects) on growth and feed efficiency

Social interaction effects are the effects that an individual has on the phenotype of its group partners and are of both genetic and environmental nature. They can induce positive (cooperation) or negative (aggressive or competition) effects on animal welfare, productivity, and health. Ignoring these effects when selecting traits that might be affected by the interaction between pen mates may lead to negative consequences on the magnitude and sign of response to selection, which depends on the genetic parameters for direct and social genetic effects. Thus, selection for individual performance may lead to strong competition when the covariance between direct and social effects is negative. The response to selection, which is determined by the sign of the covariance between an individual's phenotypic trait value and its total breeding value, could take the opposite direction of what is desired. This is particularly true for rabbits, when feed restriction is applied during fattening, which is a common practice in production farms to reduce mortality associated to digestive disorders. If animals are housed collectively in cages, as it is the case on commercial rabbit farms, it elicits competition for feed intake between cage mates. The importance of these kinds of effects has been previously evaluated in several species (e.g., pig, quail, and mink) but not in rabbits.

Social interaction effects are also very important in pigs even when they are fed ad libitum. However, estimating those effects is difficult or not possible because of problems derived from collinearity both between direct and indirect genetic effects and between pen effects and indirect genetic effects. It is therefore necessary to find appropriate models to avoid this problem.

The intensity of social interactions between animals may vary with time. For example, several studies recording the behaviour of animals in group-housed conditions have shown that aggressive behaviour is generally stronger at mixing and tends to decrease with time. However,





it is necessary to define models to analyse longitudinal records of traits affected by IGE, and to evaluate different selection strategies based on those models in terms of potential response to selection.

Feeding regimen and housing conditions regarding the number of individuals sharing the cage can lead to a genotype by environment interaction on growth and feed efficiency traits due to the impact of indirect genetic effects among cage mates (Bijma, 2011). It is necessary to assess the existence and magnitude of this interaction effect to define adequate selection strategies.

3. Selection for the animal's individual environmental sensitivity (robustness) and interaction between the genotype and feeding regimen

Specific and global robustness of animals are both strategic issues for animal breeders. The specific robustness of a particular trait, which can be defined as the genetic ability of animals to perform a homogenous production of this trait under different environmental conditions, can be quantified via statistical models that rely on the hypothesis that the residual or environmental variance of the trait is partially under genetic control (San Cristobal et al., 1998). According to this heteroscedastic model, the genetic component of the residual variance is then interpreted as a genetic sensitivity to the uncontrolled variations of the environment, providing a measure of the specific robustness of the given trait. In contrast, global robustness can be viewed as the ability of an individual to cope with adversities while maintaining its production levels for different traits, as well as a good expression of its functional traits. This global robustness can be assessed by the correlation between the genetic sensitivities of different traits to environmental variations.

Although several methods to estimate the magnitude of animal genetic sensitivity to express a specific trait in different environments have been developed, these methods have never been applied to several traits together, and the existence of a global robustness concept is still questionable. It was necessary to extend and improve the existing models to allow for the analysis of multiple traits. Consequently, the interaction between the genotype and feeding regimen at fattening could be evaluated, and ultimately some direct indicators of robustness in reproductive females and growing animals (i.e., health, mortality and longevity) could be compared.

The new statistical methodologies have been implemented in existing software. Details can be found in the published papers. In the following section, we indicate their main overall characteristics.





3. Results

3.1 Results on models to select for feed efficiency taking into account the characteristics and structure of the data

We developed and implemented the structured antedependence model (SAD) for the analysis of longitudinal records of FCR. This model fits the covariance structure of the data better than random regression models, as has been shown by others (Jaffrézic and Pletcher, 2000; Jaffrézic et al., 2004; David et al., 2017), and it requires fewer parameters to fit the covariance matrices than the random regression model. In addition, unlike the random regression models, it provides unbiased estimates of the correlation between distant measurements of the trait. However, it has been less often used in genetic analyses because of the lack of user-friendly software. Therefore, software for the analysis of longitudinal records using a SAD model has been developed by one of the members involved in the task, which is freely available at https://zenodo.org/record/1228058 (Figure 1). It allows the use of multiple-trait SAD models for the analysis of several correlated longitudinal traits such as growth and feed intake.

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	ASRemi3 for studying data with repeated measurements. It contains 3 fortran programs: saduni.f90 for single-trait SAD model; sad matrixSAD.f90 to calculate variance-covariance matrix using SAD parami			Publication date: December 1, 2016 DOI:	
	(To use saduni.f90 and sadmulti.f90 with ASReml4 see additional notes)			COI 10.5281/zenado.192036 Keyword(s): structured antedependence model, Fortran, ASRemi	
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Figure 1. Access to Fortran programs for structured antedependence (SAD) models

Using this software, we evaluated the benefit of using such model for the genetic analysis of longitudinal feed efficiency using data from 2435 growing Large White pigs from a divergent selection experiment for RFI.





We first assessed the impact of missing body weight records on the prediction of breeding values and estimation of genetic parameters for FCR. Then, different approaches were investigated to predict missing weekly BW. For the tested period, a quasi-linear interpolation based on the adjacent weeks was the best approach to deal with missing BW in our dataset, which consolidated the genetic parameter estimations compared to a data structure with missing BW (Huynh-Tran et al., 2017a). In a second step, different longitudinal models, such as random regression models, SAD and character process models were compared. The comparison focused on best-fit to the data criteria (e.g., Loglikelihood, Bayesian Information Criterion), on variance components estimations (e.g., heritability estimates, genetic variances and genetic correlations between weeks), and on the model's predictive ability (i.e., Vonesh concordance coefficients). The results showed that SAD was the most parsimonious model for FCR and RFI. The SAD model also provided similar predictive abilities as the other models. A selection criterion combining the weekly breeding values using the eigen-decomposition of the genetic covariance matrix was proposed to summarize the individual estimated breeding value (EBV) trajectory into a reduced number of parameters for practical applications to selection (Huynh-Tran et al., 2017b). In addition, we evaluated the potential of genomic information to improve the accuracy of breeding value predictions for residual feed intake, applying single step genomic approaches to the random regression and SAD models. In our dataset, prediction accuracies were low and were not improved much by genomic information. Finally, we showed that divergent selection for RFI had a major impact on the FCR and RFI profile trajectories in each line (Huynh-Tran, 2018). In conclusion, the work performed showed that selection for trajectories of feed efficiency is feasible with the current available information.

We also proposed a procedure to estimate breeding values and genetic and environmental parameters of feed efficiency from group records of feed intake and individual records of body weight gain during fattening. In this procedure, feed efficiency is defined as a conditional trait derived from elements of genetic and environmental covariance matrices. Thus, RFI (Koch et al., 1963), i.e., the difference between actual FI and that predicted on the basis of requirements for production and maintenance of body weight, would be defined as feed intake conditioned on growth and metabolic body weight (ADFI | ADG, MBW). Residual growth (Crowley et al., 2010), i.e., the difference between actual growth and that expected on the basis of maintenance energy requirements (determined from the metabolic BW) and actual feed intake, would be defined as growth conditioned on feed intake and metabolic body weight at the genetic and environmental level (ADG | ADFI, MBW). These measurements of feed efficiency are genetically and phenotypically uncorrelated with production traits. Thus, selection for some of these conditional traits does not lead to unfavourable correlated responses on production traits. The procedure has been implemented to estimate the genetic correlation between these





measurements of feed efficiency and growth rate of animals on restricted feeding (which is also a measurement of feed efficiency) to know the importance of the interaction effect between the genotype and the feeding regimen on this trait. Results suggest that different genes would be involved in feed efficiency of animals fed ad libitum or restricted.

3.2 Results on models for the analysis of social interaction effects We have developed and implemented models for the estimation of genetic and environmental parameters of direct and social effects, and estimation of the interaction between the genotype and an environmental factor (the feeding regimen in our case). Results suggest that selection of rabbits for ADG under ad libitum access to feed may completely fail to improve ADG in rabbits that are restrictively fed. This comes from the fact that social genetic effects contribute substantially to estimated total breeding values of rabbits on restricted feeding, but not situations of ad libitum feeding. This result can be seen in the plot of the distribution of the ratio of classical definition of heritability and proportion of total heritable variance relative to phenotypic variance for which the posterior mean is around 1 for ADG on ad libitum feeding and 0.5 on restricted feeding (Figure 2). Also, the genetic correlation between direct and social genetic effects for animals is negative and moderate on restricted feeding but null on ad libitum feeding (Figure 2). Therefore, selection for ADG should be performed under production conditions regarding the feeding regimen, by accounting for IGE if the

amount of feed is limited.





Figure 2.	Results	from	Piles e	t al.	(2017)
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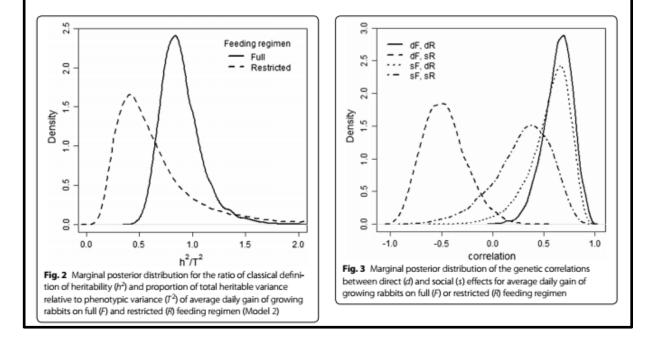
Table 5 Genetic parameters for average daily gain under different feeding regimens from the model that includes social genetic effects

Parameter ^a	Restricted f	eeding			Full feeding			
	Mean	HPD 95% ^b		MCse ^c	Mean	HPD 95% ^b		MCse ^c
TBV	3.616	0.663	6.981	0.07878	7.484	3.786	11.300	0.08072
h ²	0.033	0.017	0.051	0.00029	0.082	0.053	0.111	0.00041
T ²	0.064	0.012	0.123	0.00139	0.095	0.050	0.144	0.00102
s ²	0.0017	0.0005	0.0030	2.9e-05	0.0003	5.7e-05	0.0006	6.5e-06
ρ _{d,s}	-0.505	-0.912	-0.072	0.01059	-0.030	-0.553	0.495	0.01286
g ²	0.025	0.011	0.038	0.00017	0.023	0.011	0.036	0.00012
p ²	0.010	0.001	0.021	0.00027	0.008	0.000	0.020	0.00029
12	0.066	0.048	0.084	0.00021	0.071	0.049	0.092	0.00031
σ_p^2	56.296	54.590	58.144	0.01309	78.415	75.998	81.045	0.01620

* TBV: total breeding value; h²: variance of direct genetic effects relative to phenotypic variance; τ²: variance of TBV relative to phenotypic variance; s²: variance of social genetic effects; g²: variance of group effects relative to phenotypic variance; p²: variance of group effects relative to phenotypic variance; p²: variance of permanent animal effects relative to phenotypic variance; l²: variance of litter effects relative to phenotypic variance; σ²: variance of group effects relative to phenotypic variance; p²: variance of litter effects relative to phenotypic variance; σ²: variance of permanent animal effects relative to phenotypic variance; l²: variance of litter effects relative to phenotypic variance; σ²: phenotypic variance

variance; p⁻: variance of permanent animal effects relative to phenotypic variance; t⁻: variance of littler effects relative to phenotypic variance; $\sigma_{p^*}^{-}$: phenotypic variance ^b HPD 95%: highest posterior density interval at 95%

^c MCse: Monte Carlo standard error



We have also proposed an alternative implementation of the animal models including indirect genetic effects, aiming to alleviate collinearity through the use of feeding behaviour traits, to approach a specific degree of interaction between each pair of pen mates. The feeding behaviour traits of animals housed in groups can be obtained from electronic feeder data (as available in pigs). We have evaluated the use of feeding rate (g/min), feeding frequency (min/d), time between consecutive visits to feeder (min/d), occupation time (min/d), and an index considering all these traits to define a pair-mate specific degree of interaction. Assuming that each individual interacts differently with its mates improved the performance of models fitting indirect genetic effects and led to more accurate genetic evaluation of traits affected by indirect genetic effects, such as growth. This can be seen in the lower





deviance information criteria and lower posterior standard deviations of the posterior distributions of genetic parameters obtained from those models compared with those of the classical IGE model (Figure 3).

Figure 3. Results from Ragab et al. (2018)

	AM	AM-IGE	AM-IGE _{FR}	AM-IGE _{FF}	AM-IGE _{Fint}	AM-IGE _{OT}	AM-IGE _{ALL}
2 90 2 95	0.35 (0.13)	0.38 (0.11)	0.36 (0.11)	0.40 (0.12)	0.38 (0.12)	0.37 (0.12)	0.37 (0.11)
	_	0.004 (0.003)	0.002 (0.002)	0.001 (0.001)	0.003 (0.002)	0.005 (0.002)	0.004 (0.002
	-	-0.018 (0.02)	0.009 (0.009)	-0.005 (0.008)	0.005 (0.009)	-0.017 (0.009)	-0.025 (0.01)
_{o,as} sv orT ²	-	0.43 (0.25)	0.36 (0.15)	0.40 (0.12)	0.38 (0.13)	0.37 (0.13)	0.38 (0.11
orT^2	0.47 (0.15)	0.54 (0.29)	0.51 (0.14)	0.55 (0.13)	0.53 (0.14)	0.53 (0.14)	0.53 (0.12
1	_	_	0.51 (0.18)	0.75 (0.20)	0.65(0.20)	1.29 (0.25)	1.24 (0.30
	-	-	0.72 (0.22)	0.53 (0.19)	0.68 (0.22)	0.53 (0.21)	0.33 (0.19
	0.04 (0.02)	0.04 (0.03)	0.03 (0.02)	0.04 (0.02)	0.04 (0.02)	0.04 (0.02)	0.05 (0.03
	_	-0.39 (0.47)	0.312 (0.28)	-0.33 (0.48)	0.113 (0.31)	-0.41 (0.21)	-0.65 (0.24

AM-IGE_{FR}, AM-IGE_{FR}, AM-IGE_{FR}, AM-IGE_{Fn}, and AM-IGE_{ALL} = animal models including indirect genetic effects using feeding rate, frequency, time, interval and overall index to define the specific interaction degree between two individuals; σ_{ap}^2 = direct genetic variance; σ_{ap}^2 = indirect genetic variance; σ_{ap}^2 = total heritable variance; $\sigma_{ap,ag}^2$ = covariance between direct and indirect genetic effects; h^2 and T^2 proportion of total heritable variance in the model; T_{a1}^2 , T_{a3}^2 = T^2 at the first and third quartile of the interaction degree scale; σ_p^2 = pen environmental variance; $r_{g_{aa}}$ = genetic correlation between direct and indirect genetic effects.

Table 4 Model comparison by deviance information criteria (DIC) and the correlation between observed and predicted average daily gain of maternal Duroc pigs records ($r_{y,y}$) from an 8-fold cross-validation test, mean (SD) across folds

	AM	AM-IGE	AM-IGE _{FR}	AM-IGE _{FF}	AM-IGE _{Fint}	AM-IGE _{OT}	AM-IGE _{ALL}
DIC r _{y.ŷ}	1402.07 0.52 (0.12)	1348.69 0.53 (0.16)	1376.08 0.55 (0.09)	1338.59 0.52 (0.07)	1330.77 0.54 (0.05)	1304.74 0.56 (0.05)	1321.54 0.58 (0.04)
AM = an	imal model; AM-IGE = a indirect genetic effects						

Finally, we also have investigated how IGEs vary over time for traits under selection such as ADG on restricted feeding used to improve feed efficiency in pigs and rabbits. With this aim, we implemented a structured antedependence model that includes IGEs and we evaluated, by simulation, the response to selection on longitudinal ADG using different selection strategies. We have shown that IGE that act on ADG vary over time and that IGE have bigger magnitude during the first week after mixing. In Figure 4 it can be seen that genetic variance of IGE at week 1 was almost double than the corresponding to all other weeks.





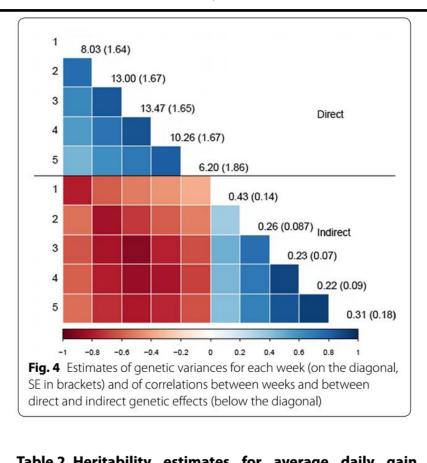




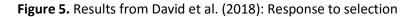
Table 2 Heritability estimates for average daily gain across weeks

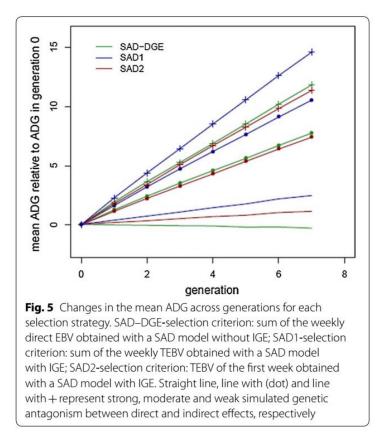
Week	Direct heritability	Indirect heritability	Total heritability
1	0.17 (0.03)	0.44 (0.13)	0.19 (0.10)
2	0.24 (0.03)	0.23 (0.07)	0.09 (0.06)
3	0.22 (0.02)	0.18 (0.06)	0.05 (0.04)
4	0.15 (0.02)	0.16 (0.06)	0.06 (0.04)
5	0.08 (0.02)	0.18 (0.11)	0.12 (0.10)

Combining total estimated breeding values (TEBV) obtained from a SAD model that includes IGE in a selection index would thus be the most effective strategy to improve longitudinal ADG when IGE occur, as can be seen in Figure 5.









3.3 Results of the analysis of genetic determinism of environmental variance

We developed a software module for the genetic analysis of bivariate heteroscedastic models. It uses the univariate DHGLM module developed by Felleki et al. (2012), and already implemented in ASRemI-4 (Gilmour et al., 2014). It is then possible to jointly estimate the parameters which affect the mean level (location parameter) and the environmental variability (dispersion parameter) of two or more traits, as well as all the cross parameters, such as the genetic correlation between the environmental sensitivities, which provides one measurement of the global robustness.

We applied this module to jointly estimate the genetic parameters for the mean and for the environmental variability of RFI and ADG in Large White pigs using data from a divergent selection experiment for RFI. We found a low negative genetic correlation between the location and dispersion parameters of RFI in these lines. This indicates that the most efficient animals (low RFI) also presented higher genetic sensitivity to micro-environmental variations for that trait. Moreover, an associated significant increase of the environmental variance of RFI was estimated in the LRFI line in response to selection, whereas no clear trend could be identified for the HRFI line, or on ADG for both lines. Finally,





we highlighted a low positive genetic correlation between dispersion parameters of RFI and ADG, which suggested that a low global robustness could exist.

The same software was used to study the relationship between genetic parameters of litter size jointly with those of BW in pig and in mice. In contrast with the previous study on RFI and ADG, the data distribution for the litter size was very different to that on BW, but the bivariate DHGLM module can cope with this issue. Most results were similar for both species and, notably, the genetic correlation between the litter size and BW dispersion was low, which comforted the suggestion of the existence of a low but significant global robustness.

4. References

- Bijma P. (2011). A General definition of the heritable variation that determines the potential of a population to respond to selection. Genetics 189: 1347-1359.
- Cai W., Casey D.S., Dekkers J.C.M. (2008). Selection response and genetic parameters for residual feed intake in Yorkshire swine. Journal of Animal Science 86: 287-298.
- Crowley J.J., McGee M., Kenny D.A., Crews Jr. D.H., Evans R.D., Berry D.P. (2010). Phenotypic and genetic parameters for different measures of feed efficiency in different breeds of Irish performance-tested beef bulls. Journal of Animal Science 88: 885–894.
- David I., Garreau H., Balmisse E., Billon Y., Canario L. (2017). Multiple-trait structured antedependence model to study the relationship between litter size and birth weight in pigs and rabbits. Genetics Selection Evolution 49: 11.
- Felleki M., Lee D., Lee Y., Gilmour A.R., Ronnegard L. (2012). Estimation of breeding values for mean and dispersion, their variance and correlation using double hierarchical generalized linear models. Genetics Research 94 (6): 307-317.
- Gilbert H., Bidanel J.P., Gruand J., Caritez J.C., Billon Y., Guillouet P., Lagant H., Noblet J., Sellier P. (2007). Genetic parameters for residual feed intake in growing pigs, with emphasis on genetic relationships with carcass and meat quality traits. Journal of Animal Science 85: 3182-3188.
- Gilmour A.R., Gogel B.J., Cullis B.R., Thompson R (2014). ASReml user guide release 4.0, VSN International Ltd, Hemel Hempstead.
- ▶ Jaffrezic F., Pletcher S.D. (2000). Statistical models for estimating the genetic basis of repeated measures and other function-valued traits. Genetics 156: 913-922.
- Kennedy B.W., van der Werf J.H., Meuwissen T.H. (1993). Genetic and statistical properties of residual feed intake. Journal of Animal Science 71: 3239-3250.





- Koch R., Swiger L., Chambers D., Gregory K. (1963). Efficiency of feed use in beef cattle. Journal of Animal Science 22: 486-494.
- Jaffrezic F., Venot E., Laloe D., Vinet A., Renand G. (2004). Use of structured antedependence models for the genetic analysis of growth curves. Journal of Animal Science 82: 3465-3473.
- ▶ Jaffrezic F., Pletcher S.D. (2000). Statistical models for estimating the genetic basis of repeated measures and other function-valued traits. Genetics 156: 913-922.
- SanCristobal-Gaudy M., Elsen J.-M., Bodin L., Chevalet C. (1998). Prediction of the response to a selection for canalisation of a continuous trait in animal breeding. Genetics Selection Evolution 30: 423-451.
- Shirali M., Varley P.F., Jensen J. (2018). Bayesian estimation of direct and correlated responses to selection on linear or ratio expressions of feed efficiency in pigs. Genetics Selection Evolution 50: 33.
- Strathe A.B., Mark T., Nielsen B., Do D.N., Kadarmideen H.N., Jensen J. (2014). Deriving genomic breeding values for residual feed intake from covariance functions of random regression models., Proceedings of the 10th World Congress of Genetics Applied to Livestock Production, 17 22 August 2014, Vancouver, British Columbia, Canada.

5. Conclusions

New models and procedures for the genetic evaluation of feed efficiency and robustness have been proposed and tested on different datasets. These models take into account the constraints of different livestock species, resulting in specific characteristics and structure of the data regarding the presence of missing values, the correlation between repeated measures of the same trait, and the existence of genetic and environmental effects of cage/pen mates on the individual trait. The estimations obtained showed that the developments give access to breeding values for feed efficiency in cases when they were not available before (group-housed animals), or refined their estimations by accounting for the data structure. Newly developed software or routines in existing software have been developed and made publicly available for the implementation of such models for selection on growth and feed efficiency.

Within the Feed-a-Gene project some of the developments will be further evaluated to provide recommendations for their use in routine evaluation (i.e., user-friendliness and speed of computation are major requirements) or their use to refine the understanding of the genetic architecture of the traits in R&D projects, based on the models properties, and the potential of their optimization. Part of





these models are also tested in the project for a practical demonstration of their advantages in rabbits and pigs.

6. Publication list

- Huynh-Tran V.H., Gilbert H., David I. (2017a). Genetic structured antedependence and random regression models applied to the longitudinal feed conversion ratio in growing Large White pigs. Journal of Animal Science 95: 4752-4763.
- Huynh-Tran V.H., Gilbert H., David I. (2017b). How to improve breeding value prediction for feed conversion ratio in the case of incomplete longitudinal body weights. Journal of Animal Science 95:39-48.
- Huynh-Tran V.H. (2018). New genetic longitudinal models for feed efficiency (Thèse de doctorat, Institut National Polytechnique, FRA). 123 p. http://prodinra.inra.fr/record/451583.
- David I., Sánchez J.P., Piles M. (2018). Structured antedependence model for longitudinal analysis of direct and social effects on the average daily gain in growing rabbits. In: Book of Abstracts of the 69th Annual Meeting of the European Federation of Animal Science. Dubrovnik, Croatia, 27- 31 August 2018.
- David I., Sánchez J.P., Piles M. (2018). Longitudinal analysis of direct and indirect effects on the average daily gain in growing rabbits using a structured antedependence model. Genetic Selection Evolution 50: 25.
- David, Ingrid. (2017, September 19). New fortran programs for genetic studies with structured antedependence models (Version V2). Zenodo. http://doi.org/10.5281/zenodo.1228058.
- Sánchez J.P., Ramon J., Rafel, O., Ragab M., Piles M. (2016). Using collective feed intake data to select for feed efficiency on full or restricted feeding regimen. In: Proceedings of the 11th World Rabbit Congress, June 15-18, 2016, Qingdao, China.
- Piles M., Ramon J., Rafel O., Ragab M., Sánchez J.P. (2016). Mejora de la eficiencia alimentaria de gazapos criados en grupos e interacción entre el genotipo y el régimen alimentario en estas condiciones de alojamiento. XVIII Reunión Nacional Sobre Mejora Genética Animal. June 2-3, 2016. Valencia, Spain.
- Piles M., Sánchez J.P. (2019). Using group records of feed intake data to select for feed efficiency. Journal of Animal Breeding and Selection (submitted).
- Piles M., David I., Ramon J., Canario L., Rafel O., Pascual M., Ragab M., Sánchez J.P. (2017). Interaction of direct and social genetic effects with feeding regime in growing rabbits. Genetics Selection Evolution 49:58.





- Ragab M., Piles M., Quintanilla R., Sánchez J.P. (2019). Indirect genetic effect model using feeding behaviour traits to define the degree of interaction between mates: an implementation in pigs growth rate. Animal 13: 231-239.
- Ragab M., Piles M., Quintanilla R., Sánchez J.P. (2016). Alternative consideration of social genetic effects models in Duroc pigs. XVIII Reunión Nacional Sobre Mejora Genética Animal. June 2-3, 2016. Valencia, Spain.
- Ragab M., Piles M., Sánchez J.P. (2016). Alternative consideration of social genetic effects models in Duroc pigs. In: Book of Abstracts of the 67th Annual Meeting of the European Federation of Animal Science. Belfast, UK, 29 Aug – 2 Sept 2016.
- Bodin L., Formoso-Raferty N., Gilbert H. (2018). Genetic bases of individual performance variation in pigs. In: Book of Abstracts of the 69th Annual Meeting of the European Federation of Animal Science. Dubrovnik, Croatia, 27-31 August 2018.
- Formoso-Rafferty N., Cervantes I., Sánchez J.P., Gutierrez J.P., Bodin L. (2017). Feed restriction on growth of mice divergently selected for birth weight environmental variability. In: Book of Abstracts of the 68th Annual Meeting of the European Federation of Animal Science. Tallinn, Estonia, August 28 – September 1, 2017.
- Formoso-Rafferty N., Cervantes I., Sánchez J.P., Gutierrez J.P., Bodin L. (2017). Efecto de la restriccion alimentaria sobre el crecimiento en dos lineas divergentes para variabilidad ambiental del peso al nacimiento en ratones. Asociación Interprofesional para el Desarrollo Agrario, XVII Jornadas sobre Producción Animal.



