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Product versus additive model for studying artificial insemination results in several livestock populations

I. David,^{*1} M. J. Carabaño,[†] L. Tusell,[‡] C. Diaz,[†] O. González-Recio,[†]
E. López de Maturana,[†] M. Piles,[‡] E. Ugarte,[§] and L. Bodin^{*}

^{*}INRA UR 631 Station d'Amélioration Génétique des Animaux, 31320 Castanet-Tolosan, France;

[†]Departamento de Mejora Genética Animal, INIA, Carretera de La Coruña km 7.5, 28040 Madrid, Spain;

[‡]Unitat de Cunicultura, Institut de Recerca i Tecnologia Agroalimentàries, Torre Marimon s/n, 08140, Caldes de Montbui, Barcelona, Spain; and [§]Neiker, 01000 Vitoria-Gasteiz, Spain

ABSTRACT: Two models can be used for studying binary results of AI. The additive threshold model proposes an underlying variable as summing the environmental and genetic effects from the 2 individuals involved in the mating, and the product threshold model assumes that the conditional probability of AI success is the product of the probabilities of success of 2 unobserved binary phenotypes (one is the male fertility; the other is the female fertility). The purpose of this paper is to compare the predictive ability of the product and the additive threshold models for studying AI results and to compare results obtained with the 2 models in 3 different species: cattle, sheep, and rabbits. Results showed that the predictive ability of the product model is similar to the additive model in sheep and rabbits but worst in cattle (percentage of wrong prediction = 42, 27, and 35% in the additive model; 43, 28, and 47% in the product model in sheep, rabbits, and cattle,

respectively). Even when the 2 models have similar performance, they differed in their EBV (for instance, Pearson correlation between EBV predicted with the 2 models = 0.46 in sheep for male fertility). The product model can determine which sex is responsible for an AI failure. In sheep, the female was the responsible in 94% of the cases and male in 2% of them; in rabbits, the female was the responsible in 54% of the cases and the male in 39% of them. Different estimates of probabilities for male and female fertility success obtained with the product model in the 3 species suggest that male and female fertilities behave differently depending on the species and the uniqueness of the data sets. Although product model seems to provide additional information in the fertility process, further research is needed to understand the worst performance of the product model in cattle.

Key words: additive model, fertility, predictive ability, product model

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INTRODUCTION

The outcome of AI is affected by factors related to the male, the female, or factors common to both sexes. The outcome of AI may be registered as a binary code indicating pregnancy or nonpregnancy. The most common approach in animal genetic models for such a binary trait is the additive threshold model, which proposes a underlying variable resulting from the addition of environmental and genetic effects from the 2 individuals involved in the mating (Varona and Noguera, 2001; Piles et al., 2005). However, some authors have pointed out that the combination of those sources of variation may

not be purely additive (Speirs et al., 1983). Recently, David et al. (2009) proposed a product threshold model assuming that conception in a given mating is the product of the outcome of each mating member. Hence, the conditional probability of AI success is the product of the probabilities of the success of 2 unobserved binary phenotypes (one is the male fertility; the other is the female fertility). This assumption has several advantages over that assumed in the additive model. First, it describes in a better manner the biological mechanism of the mating. Second, it provides distinct estimates of environmental effects affecting each of the 2 unobserved phenotypes, and as a result allows more information to be extracted from the data. David et al. (2009) showed the feasibility of this model in a genetic context using simulated data. However, the product threshold model has not been applied to real data yet. The purpose of this study was to compare the performance, in terms of

¹Corresponding author: Ingrid.David@toulouse.inra.fr
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predictive ability, of the product and additive threshold models for studying AI result and to compare results obtained with the 2 models in 3 data sets of different species: cattle, sheep, and rabbit. Differences between them originating not only from the specific characteristics of the species, but also from the different processes and conditions for AI (e.g., ejaculate selection, dose preparation, hormonal treatments) applied.

MATERIALS AND METHODS

Animal Care and Use Committee approval was not obtained for this study because the data were obtained from an existing database.

Materials

Artificial insemination data corresponding to the 3 species were used for the analysis (Table 1). Cattle data were provided by the regional Holstein Associations from Basque Country, Navarra, and Girona. Data were extracted from the November 2008 routine genetic evaluation for female fertility implemented in the north-western population of Spanish Holstein-Friesian cattle and included insemination records from 1995 to September 2008. As in most cattle populations, commercial frozen semen is used for AI in this population. Normally, bull semen is screened to discard ejaculates with low motility or abnormal sperm at collection or after freezing and thawing the samples. Bull ejaculates from the same day of collection are mixed and diluted in a proportion that ensures a minimum amount of motile spermatozoa in the AI straw. Estrus synchronization is becoming a frequent practice, but no recording of its incidence is carried out in this population. A service record was defined as success (1) if a subsequent calving existed and the corresponding gestation length period was within the interval 272 to 292 d. The insemination was considered as a failure (0) when additional inseminations within the same lactation existed or no subsequent calving was registered. Restrictions and rules for validating records were applied to ensure the quality of reproductive data following González-Recio and Alenda (2005). In addition, at least 20 observations per region-year and herd-year groups were required. Service sires with less than 50 AI observations were removed from the data set. Failure and success percentages per region-year, herd-year, and service sire groups were restricted to be between 15 and 85% to avoid extreme category problems (Moreno et al., 1997). The editing procedure reduced the initial data set to 501,284 AI records from 183,833 cows. Data from all lactations from a cow were present. The phenotypic probability of AI success was 37%.

French sheep data came from a specific database built by the ANIO (Association National des Centres d'Insémination Ovine), which combines information from AI centers (information on males and characteris-

tics of the semen) and the French national performance recording scheme (pedigree information and ewe performances). For this species, records of inseminations in the Manech Tête Rousse breed performed between 2000 and 2004 were used in the analysis. After male collection, semen was selected based on motility (0 to 5 scale, ejaculates with motility <4 were discarded) and diluted to obtain AI doses with standardized concentration (1.2×10^6 spermatozoa/mL). Synchronized ewes were inseminated (cervical insemination) a few hours (1 to 8) after male collection with fresh semen. The AI outcome was defined as success (1) if lambing occurred 5 mo after insemination and failure (0) otherwise. After discarding service sires with less than 150 AI, 13,275 records were retained for the analysis; the observed probability of AI success was 51%.

Rabbit data came from a population of a sire line selected for growth rate (Caldes line: Gómez et al., 2002). Data collected from June 2003 to December 2007 were used in this study. For the preparation of AI doses, ejaculates containing urine and calcium carbonate deposits were discarded, and gel plugs were removed. No evaluation of seminal characteristics was performed. Ejaculates were diluted 1:4 immediately after collection to obtain the AI doses. Female estrus and ovulation were induced by hormonal treatment. Artificial insemination doses of 0.5 mL were applied within 1 h after preparation on females from the same sire line, also reared in the nucleus of selection. Success or failure of AI was obtained from the diagnosis of pregnancy made by palpation 14 d after AI. Information on the day of parturition helped to confirm the previous diagnosis of palpation. A total of 6,543 AI records were used for the analysis. The observed probability of AI success was 72%.

Methods

Additive and product threshold models suppose different assumptions. In the additive threshold model, the observed phenotype is linked (probit link function) to a liability which is the sum of all genetic and environmental factors affecting male and female fertility. Thus, under the additive model the conditional probability of success given the genetic and environmental factors can be expressed as

$$\Pr(\mathbf{y} = 1 | \theta) = \Phi(\mathbf{X}_f \mathbf{b}_f + \mathbf{X}_m \mathbf{b}_m + \mathbf{X}_c \mathbf{b}_c + \sum_i \mathbf{K}_i \mathbf{f}_i + \sum_n \mathbf{M}_n \mathbf{m}_n + \sum_j \mathbf{L}_j \mathbf{c}_j + \mathbf{Z}_f \mathbf{u}_f + \mathbf{Z}_m \mathbf{u}_m + \mathbf{W}_m \mathbf{p}_m + \mathbf{W}_f \mathbf{p}_f),$$

where \mathbf{y} is the vector of the binary results of inseminations; $\Pr(\mathbf{y} = 1 | \theta)$ is the conditional (given the genetic and environmental factors variables θ) probability of AI success. The $\Phi(\cdot)$ is the standard cumulative distribution function of the normal distribution. The

Table 1. Description of sheep, cattle, and rabbit data

Item	Sheep	Cattle	Rabbit
No. of females	12,102	133,883	2,601
No. of males	38	949	300
No. of AI records	13,275	501,284	6,543
No. of animals in the pedigree	37,213	216,373	3,302
No. of observations per male ¹	350	528	21.8
	[217, 423]	[133, 369]	[9, 30]
No. of observations per female ¹	1.1	3.7	2.5
	[1, 1]	[2, 5]	[1, 3]
No. of different inseminated females per male ¹	347	443	19
	[216, 421]	[120, 326]	[9, 26]
No. of different males per female ¹	1.0	3.1	2.2
	[1, 1]	[1, 4]	[1, 3]
Probability of AI success per male ¹	0.52	0.37	0.70
	[0.49, 0.53]	[0.32, 0.42]	[0.60, 0.83]
Probability of AI success per female ¹	0.51	0.45	0.69
	[0, 1]	[0.17, 0.67]	[0.50, 1.00]
Observed probability of AI success	0.51	0.37	0.72

¹Values presented as mean [P25, P75]. P25, P75: 25th and 75th percentile.

\mathbf{b}_f , \mathbf{b}_m , and \mathbf{b}_c are vectors of systematic effects related to the female, the male, or common to both sexes, respectively. The \mathbf{u}_f and \mathbf{u}_m are vectors of female and male fertility additive genetic effects, respectively. The \mathbf{p}_m and \mathbf{p}_f correspond to the vectors of male and female random permanent environmental effects; \mathbf{f}_i , \mathbf{m}_n , and \mathbf{c}_j are the random vectors of the i th, n th, and j th effects specific to the female, male, or common to both sexes, respectively. The \mathbf{X}_f , \mathbf{X}_m , \mathbf{X}_c , \mathbf{Z}_f , \mathbf{Z}_m , \mathbf{W}_f , \mathbf{W}_m , \mathbf{K}_i , \mathbf{M}_n , and \mathbf{L}_j are corresponding known incidence matrices. On the other hand, the product threshold model considers that the conditional probability of AI success is the product of the probability of success of 2 binary unobserved phenotypes: the male and female fertilities (David et al., 2009). The 2 corresponding liabilities are the sum of genetic and environmental factors specific to the considered mate-sex and also those common to both sexes:

$$\Pr(\mathbf{y} = 1 \mid \theta) = \Phi(\mathbf{X}_f \mathbf{b}_f + \mathbf{X}_c \mathbf{b}_c + \sum_i \mathbf{K}_i \mathbf{f}_i + \sum_j \mathbf{L}_j \mathbf{c}_j + \mathbf{Z}_f \mathbf{u}_f + \mathbf{W}_f \mathbf{p}_f) \times \Phi(\mathbf{X}_m \mathbf{b}_m + \mathbf{X}_c \mathbf{b}_c + \sum_n \mathbf{M}_n \mathbf{m}_n + \sum_j \mathbf{L}_j \mathbf{c}_j + \mathbf{Z}_m \mathbf{u}_m + \mathbf{W}_m \mathbf{p}_m).$$

In both models, all random effects were assumed to be distributed following centered normal distributions with (co)variance matrices equal to $\begin{bmatrix} \sigma_{u_m}^2 & \sigma_{u_f u_m} \\ \sigma_{u_f u_m} & \sigma_{u_f}^2 \end{bmatrix} \otimes \mathbf{A}$ for the correlated genetic effects and $\mathbf{I}_q \sigma_q^2$ for the other random effects q ($q = \mathbf{c}_j, \mathbf{m}_n, \mathbf{f}_i, \mathbf{p}_f$, or \mathbf{p}_m), where \mathbf{A} is the known relationship matrix and \otimes represents the Kronecker product, \mathbf{I}_q is an identity matrix of appropriate dimension, and σ_q^2 is the corresponding variance for

the effect q . Nongenetic random effects were assumed to be independent of each other and of genetic effects.

Heritabilities on the observed scale were computed following the transformation proposed by Dempster and Lerner (1950): in the additive threshold model,

$$h_{female_fertility}^2 = \frac{\sigma_{u_f}^2}{\sigma_T^2} \times z^2 / [P_{obs} \times (1 - P_{obs})] \quad \text{and} \\ h_{male_fertility}^2 = \frac{\sigma_{u_m}^2}{\sigma_T^2} \times z^2 / [P_{obs} \times (1 - P_{obs})], \quad \text{for the female and male fertility, respectively, where } P_{obs} \text{ is the observed probability of AI success. The total variance } \sigma_T^2 \text{ was calculated as } \sigma_T^2 = \sigma_{u_f}^2 + \sigma_{u_m}^2 + \sigma_{p_f}^2 + \sigma_{p_m}^2 + \sum_i \sigma_{f_i}^2 + \sum_n \sigma_{m_n}^2 + \sum_j \sigma_{c_j}^2 \text{ and } z \text{ is the ordinate of a standard normal distribution function corresponding to a threshold equal to } \Phi^{-1}(P_{obs}).$$

For the product threshold model,

$$h_{female_fertility}^2 = \frac{\sigma_{u_f}^2}{\sigma_{T_1}^2} \times z_f^2 / [P_{obs} \times (1 - P_{obs})] \quad \text{and} \\ h_{male_fertility}^2 = \frac{\sigma_{u_m}^2}{\sigma_{T_2}^2} \times z_m^2 / [P_{obs} \times (1 - P_{obs})], \quad \text{for female and male fertility, respectively. Where } \sigma_{T_1}^2 = \sigma_{u_f}^2 + \sigma_{p_f}^2 + \sum_i \sigma_{f_i}^2 + \sum_j \sigma_{c1_j}^2 \text{ and } \sigma_{T_2}^2 = \sigma_{u_m}^2 + \sigma_{p_m}^2 + \sum_n \sigma_{m_n}^2 + \sum_j \sigma_{c2_j}^2. \text{ The } z_f \text{ and } z_m \text{ are the ordinates of standard normal distribution functions corresponding to thresholds equal to } \Phi^{-1}(P_f) \text{ and } \Phi^{-1}(P_m). \text{ The } P_f, P_m \text{ are the probabilities of success for the unobserved phenotypes of female and male fertility, respectively.}$$

Table 2. Effect included in models for sheep, cattle, and rabbit data

Type	Effect	No. of levels		
		Sheep	Cattle	Rabbit
Systematic				
Male effect	Insemination No.	—	5	—
	Motility	12	—	—
Female effect	Rank of insemination	—	5	—
	Interval with previous birth	7	4 ¹	—
	Region × year	—	94	—
	Milk production	4	—	—
	Physiological status of the female	3	—	3
	Age	7	—	—
	Lactation × age	—	16	—
	Previous synchronization	2	—	—
	No. of previous synchronizations	8	—	—
Common effect	Day × inseminator	—	—	22
Random				
Male effect	Genetic male fertility	37,213	216,373	3,302
	Permanent environmental effect	38	949	300
	Permanent environmental effect × day	—	—	1,232
	Inseminator	37	—	—
Female effect	Genetic female fertility	37,213	216,373	3,302
	Permanent environmental effect	—	133,883	2,601
	Herd × year	626	—	—
Common effect	Year × season	31	—	—
	Herd × year	—	6,567	—

¹Interval from calving to first AI.

Implementation

Data sets from the 3 species were analyzed using the additive and product threshold models. In each species, the same random, systematic, and genetic effects were included in both models. The systematic effects varied depending on the species (Table 2). Under the product model, effects were considered for each data set as specific to the male, to the female, or common to both sexes.

In a first step, additive and product threshold models were compared based on their ability of predicting new records as follows: 75% of records within species were used to estimate parameters, and the new records were predicted in the remaining 25%. Five replicates of this design were randomly sampled. Different statistics were computed to evaluate the predictive ability of the 2 models: a) the percentage of wrong prediction; b) the mean square error of prediction (**MSEP**) defined as

$$MSEP = \frac{1}{n} \sum_i^n [y_i - \hat{P}(y_i = 1)]^2, \text{ where } y_i \text{ and } \hat{P}(y_i = 1)$$

correspond to the observed AI outcome and predicted probability of success, respectively, and n is the number of data in a testing subset; c) the sensitivity of the prediction defined as the probability to predict a success given that the observation is a success; d) the specificity or the probability to predict a failure given that the observation is a failure; e) the negative predictive value defined as the probability to observe a failure given that the prediction is a failure; and f) the positive predictive value or the probability to observe a success given that the prediction is a success.

In a second step, the estimated parameters obtained with the 2 models on the whole data set for each species were compared. The Pearson correlation between predicted breeding values and the percentage of animals in common in the top and bottom 10% animals were used to evaluate the differences in results between the 2 models.

Estimates were obtained using a Bayesian approach via Gibbs sampling. The core of the program is the TM (threshold model) software developed by Legarra et al. (2008). Flat priors were used for systematic effects and variance components, and starting values were randomly sampled. The Gibbs sampler analysis was implemented using one single chain consisting of 300,000, 400,000, and 500,000 iterations in sheep, cattle, and rabbits, respectively. After discarding the first 30,000 (sheep) or 50,000 (cattle and rabbit) iterations, samples of the parameters of interest were saved every 100 iterations. Inferences on the marginal posterior distributions were directly performed from the retained samples. Posterior means were used as parameter estimates.

RESULTS

Table 3 shows the predictive ability estimates for each model obtained for each criterion used. The MSEP estimates were similar between product and additive models within species. The percentages of wrong prediction for both models were in agreement for sheep and rabbit; however, a smaller percentage was obtained with the additive model in dairy cattle (35 vs. 47%). The negative and positive predictive values are quite simi-

Table 3. Predictive ability of the product and threshold models in sheep, cattle, and rabbits

Item	Sheep		Cattle		Rabbit	
	Product	Additive	Product	Additive	Product	Additive
% of wrong prediction	43	42	47	35	28	27
MSEP ¹	0.24	0.24	0.22	0.22	0.16	0.15
Sensitivity	0.71	0.54	0.69	0.19	0.99	0.98
Specificity	0.45	0.59	0.44	0.90	0.06	0.10
Negative predictive value	0.70	0.65	0.73	0.68	0.66	0.66
Positive predictive value	0.47	0.47	0.40	0.50	0.72	0.73

¹MSEP = mean square error of prediction.

lar between models, whereas the product model tended to be more sensitive and less specific than the additive one. Between species, the MSEP and percentage of wrong prediction were, for both models, less in rabbits than in sheep and cattle. In both models, sensitivity increased from cattle (additive = 0.19, product = 0.69), to sheep (additive = 0.54, product = 0.71) and rabbits (additive = 0.98, product = 0.99), whereas specificity decreased (cattle: 0.90 and 0.44, sheep: 0.59 and 0.45, rabbits: 0.10 and 0.06 for additive and product models, respectively). The negative predictive values were in the same range among species, whereas the positive predictive value was greater in rabbit than in sheep or cattle.

Results obtained for the whole data sets (Table 4) showed that the probability of success estimates for the unobserved phenotypes obtained from the product model were quite different between species. The probability of success of male fertility was greater than for female fertility in sheep (0.97 vs. 0.52), less in cattle (0.57 vs. 0.65), and similar in rabbits (0.87 vs. 0.83).

Within species, heritability estimates on the underlying scale in the product model were greater than in the additive model (ratio ranging from 1 to 21). The estimated heritabilities on the observed scale were low for both traits (<0.11) in all species and models. The heritabilities on the observed scale were greater (\geq) for the product than for the additive model (ratio ranging from 1 to 5), but generally, credibility intervals overlap.

The posterior means of the genetic correlations between male and female fertilities were estimated with reduced credibility with either of the models or species, as credibility intervals ranged from -0.59 to 0.68 in sheep and from -0.72 and 1 in rabbit with the product model. Smaller credibility interval was found in dairy cattle (ranging from -0.24 to 0.15), suggesting a null genetic correlations between male and female fertilities.

The correlations between EBV for all animals in the pedigree obtained with the additive or product threshold models were large (ranging from 0.93 to 0.99 depending of the species) except for the male fertility in sheep (0.46). The same correlations calculated only with animals having records were generally greater (0.75 for male fertility in sheep). In accordance with the correlations, the percentage of animals in common in

the 10% best/worst animals is large (≥ 0.73), except for male fertility in sheep (≤ 0.43).

DISCUSSION

Due to the process of editing data, the observed probabilities of AI success are slightly less than the one previously reported for the same breed in sheep (0.57; David et al., 2008) but in accordance with previous studies in rabbits (El Gaafary and Marai, 1994).

Under the product model, environmental factors can be distinctly attached to male, female, or to both, which cannot be done under an additive model. In our study, the assignment of environmental factors to male or female fertility, or both, has been somehow arbitrary. This choice is straightforward for some effects (e.g., age of the male, milk production) but not for all (e.g., inseminator). Consequently, the same factors did not affect the same trait depending of the species. For instance, the herd \times year effect is linked to the female in sheep and to both sexes in cattle. The relevance of alternative effects acting on male or female fertility can be explored by classical model comparison techniques. We explored for a subset of the rabbit data the selection of effects in the product model. We first estimated parameters in a saturated model including all factors for male and female fertility. We removed step-by-step factors for which all credibility intervals included 0. The final model obtained is consistent in the face of the factors included in both sides, illustrating the ability of the product model to correctly assign a factor as acting on male or female fertility, or both (results not shown). This was not carried out in our study for all species due to computing limitations and because it is not likely to affect the comparison between product and additive models, which was our goal. However, it has to be performed if the objective of the study is to analyze the factors influencing fertility.

The sampling method that we used to evaluate the predictive ability of the 2 models does not correspond to a standard 5-fold cross-validation (Shao, 1993). In this paper, random sampling was repeated 5 times, making sure that all random and systematic effect levels (except female permanent effect) in the testing sample were estimated previously in the training sample. This sampling method was used to avoid unexpected

Table 4. Posterior means and credibility interval at 95% [in brackets] of the probability of success for the unobserved phenotypes, genetic variances, heritabilities, and correlation between breeding values obtained with the additive and threshold models applied to the whole data set in sheep, cattle, and rabbits

Item	Sheep		Cattle		Rabbit	
	Product	Additive	Product	Additive	Product	Additive
$P(\text{female fertility} = 1)$	0.52 [0.51, 0.54]	—	0.65 [0.63, 0.68]	—	0.83 [0.77, 0.90]	—
$P(\text{male fertility} = 1)$	0.97 [0.95, 0.98]	—	0.57 [0.54, 0.60]	—	0.87 [0.80, 0.93]	—
Genetic variance of female fertility	0.22 [0.15, 0.30]	0.19 [0.13, 0.27]	0.16 [0.13, 0.19]	0.04 [0.03, 0.05]	0.12 [<0.01, 0.33]	0.04 [<0.01, 0.09]
Genetic variance of male fertility	2.30 [0.20, 6.18]	0.02 [0.01, 0.03]	0.02 [0.01, 0.03]	0.01 [0.01, 0.01]	0.47 [0.03, 1.24]	0.05 [0.01, 0.09]
Heritability on the underlying scale of female fertility	0.17 [0.12, 0.22]	0.15 [0.10, 0.20]	0.11 [0.09, 0.13]	0.04 [0.03, 0.04]	0.08 [<0.01, 0.18]	0.03 [<0.01, 0.06]
Heritability on the underlying scale of male fertility	0.36 [0.06, 0.63]	0.02 [<0.01, 0.03]	0.02 [0.01, 0.03]	0.01 [<0.01, 0.01]	0.17 [0.03, 0.36]	0.04 [0.01, 0.07]
Heritability on the observed scale of female fertility	0.11 [0.08, 0.14]	0.09 [0.07, 0.13]	0.06 [0.05, 0.07]	0.02 [0.02, 0.03]	0.04 [<0.01, 0.10]	0.02 [<0.01, 0.03]
Heritability on the observed scale of male fertility	0.01 [<0.01, 0.02]	0.01 [<0.01, 0.02]	0.01 [<0.01, 0.02]	0.01 [<0.01, 0.01]	0.10 [0.02, 0.20]	0.02 [<0.01, 0.04]
Genetic correlation	0.04 [−0.59, 0.68]	0.21 [−0.29, 0.72]	−0.04 [−0.24, 0.15]	−0.05 [−0.25, 0.17]	0.21 [−0.72, 1.00]	0.31 [−0.60, 0.99]
Correlation between female fertility EBV, all animals/females with records	0.99/0.99		0.99/0.99		0.93/0.93	
Correlation between male fertility EBV, all animals/males with records	0.46/0.75		0.98/0.99		0.96/0.96	
Percentage of animals in common in the top 10% best, bottom 10% worst animals for female/male fertility	0.92, 0.92/0.22, 0.43		0.91, 0.86/0.91, 0.80		0.73, 0.76/0.81, 0.81	

consequences of missing estimation for the additive or product models. Nonetheless, a 5-fold cross-validation was performed with the rabbit data and provided results very close to those presented in this study (results not shown). Within species, similar results obtained for MSEP and percentage of wrong prediction in rabbits and sheep show that product and additive threshold models have the same predictive ability. Nonetheless, as reported in previous studies for comparison with other models (Vazquez et al., 2009a,b), predictive ability of the models is different depending on the observed result. Thus, the product model was more sensitive and less specific than the additive one. Therefore, the product model had a better ability to predict a success and a worse ability to predict a failure than the additive model. For cattle, results are in favor of the additive threshold model that has a smaller percentage of wrong prediction. Even if models have similar predictive ability in sheep and rabbits, they provided different breeding values and animals will not be identically selected

with the 2 models, especially for male fertility in sheep. These results suggest that either the additive or the product model may provide inaccurate predictions for male fertility. As true breeding values are unknown, further studies are necessary to determine what model is more accurate in predicting male fertility. An experimental selection with the 2 models, which could be carried out in rabbits, could be a way to give an answer to this question.

Heritabilities estimated with the additive threshold model were small for both traits, but in accordance with previous studies (González-Recio and Alenda, 2005; Piles et al., 2005; David et al., 2007). Heritabilities obtained with the product model cannot be related to the accuracy of the estimation or the genetic progress in the same manner as in the additive model. Therefore, estimation of heritabilities obtained with the 2 models cannot be properly compared, even if they are expressed in the observed scale. Further investigations are needed to give a practical interpretation of the heri-

tability in the product threshold model. Conversely to the heritabilities, the genetic correlation between male and female fertilities can be compared across models. The 95% credibility intervals for all estimates were very large, and therefore we could not observe any differences between estimates. This result was in accordance with previous studies showing a wide range of genetic correlations between male and female fertilities: from -0.53 [$-0.86, -0.01$] (Varona and Noguera, 2001) to 0.73 [$-0.36, 0.99$] (Piles et al., 2005). However, in cattle, where a narrower credibility interval was obtained, the genetic correlation between male and female fertility seems to be small or null. Thus, the nature of this genetic correlation between both sexes for fertility still seems to be unclear and could differ between species.

Estimated probabilities of success for the unobserved phenotypes indicated that an AI failure was specifically due to female fertility problems for 94, 32, or 54% of the cases in sheep, cattle, and rabbits, respectively, and is specifically due to male fertility problems for 2, 44, and 39% of the cases in sheep, cattle, and rabbits, respectively. Therefore, the product model reports that an AI failure is mainly due to an impairment in female fertility in sheep and rabbits and due to an impairment in male fertility in cattle. It is difficult to compare these results with those reported previously in the literature. Actually, the only species where origin of infertility is well documented is humans after natural mating (Forti and Krausz, 1998). Forti and Krausz (1998) reported that in 35% of cases, infertility is mainly due to a female factor, in 30% to a male factor, in 20% to abnormalities detected in both partners, and in 15% of cases no diagnosis can be made after a complete investigation. Male fertility is supposed to behave differently between the 3 studied species. The uniqueness in the processes for preparing doses and insemination techniques may explain these differences. In sheep, semen is strongly selected upon its motility and sperm concentration; the doses have the same number of spermatozoa and are deposited in the female tract less than 6 h after collection (fresh semen). This process allows a control of main environmental factors reported in the literature as affecting male fertility (Briois and Guerin, 1995; Fernandez-Abella et al., 2003; Foote, 2003; Donovan et al., 2004). Conversely, there was no ejaculate selection upon its seminal characteristics (except urine or calcium deposits) in this study for rabbits, and there was no standardization of the dose concentration. This process may induce a decrease in the potential sperm fertility and explain the relative importance of the male in the AI failure. In dairy cattle, we observed the least probability of success for the male fertility. In this species, the sperm selection process is similar to the one performed in sheep but inseminations are performed with frozen semen. This difference may explain the greater relative importance of the male in AI failure in cattle. For female fertility, ovulation is induced after insemination in rabbits; therefore, the probability

that the oocyte is released at the optimum time in the female reproductive tract is very large, which might explain the greatest percentage of female fertility success observed in this species (0.83). In sheep, females were inseminated regardless to expression of estrus, although they were estrus synchronized, which might explain the decreased probability of fertility success (0.52). On the other hand, the increased estimate of probability of success for female fertility in cattle (0.65) is surprising because female fertility problems have been largely reported as an explanation of the decrease of AI success observed in dairy cattle for a long time (Lucy, 2001).

The objective of this study was to evaluate in 3 species the performance of the product threshold model for the modeling of the outcome of AI. We have shown that its predictive ability is similar to the additive model in sheep and rabbit and slightly worse than the additive model in dairy cattle. When it holds, the product model has the advantage of extracting more information from the data than the additive threshold model. It is possible to evaluate which sex is responsible for an AI failure, and this would help to improve fertility. However, product model suffers from some drawbacks. In some cases a strong editing data process has to be done to ensure convergence (cattle and sheep in this study to avoid extreme category problems). Furthermore, interpretation of genetic parameters estimates is not straightforward and it is necessary to work on the estimation of the genetic progress in this model. At present, estimations are obtained using a Bayesian approach and the computing time is very long, which avoids the use of this model for large data sets. Finally, we think that the product model is, at present, an interesting model to test for studying AI results, or other traits with the same kind of associated binary unobserved phenotypes, in an experimental context.

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