Optimized management of genetic variability in selected pig populations

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Introduction

Selection induces losses of genetic variability and increases of inbreeding rates, both being detrimental to the long-term sustainability of breeding schemes. Pig breeding schemes are faced with major risks, due to fast turn-over of generations and species prolificacy that allows strong selection pressures. In these conditions, appropriate management methods are required for maximizing genetic gain at fixed inbreeding rate or alternatively minimizing inbreeding rate at fixed genetic gain. For the last 20 years, corresponding research in quantitative genetics has been very active, resulting in efficient proposals based on considering long term contributions (Woolliams et al. 2002). A tentative short survey of the successive approaches over history was carried out by Colleau et al. (2004a) and Colleau & Moureaux (2006). In fact, selection schemes are very complex and divided into distinct steps, where implementation of optimization principles needs to be customized accordingly. For dairy cattle, Colleau et al. (2004b), Colleau & Moureaux (2006) showed, based on field data provided by the three major French dairy cattle breeds, how such an adaptation might be envisioned for four successive steps.

For pig selection, two major steps are involved. First, selecting males to be mated to already selected females for breeding, modulating their use and determining appropriate mates (referred to as ‘service’ step hereafter). Second, choosing replacement animals to be used for breeding and animals to be...

Keywords
Coancestry; estimated breeding value; inbreeding; optimization; pig.

Summary

Controlling the increase of coancestry and inbreeding coefficients in selected populations is made possible through calculation of the optimal contributions allowed to breeding animals, given the current situation with regard to genetic diversity, and further, through optimal design of matings. The potential of such an approach for pig breeding was tested by retrospective optimization on the French Landrace population in reference to the matings actually carried out during a 21-week test period. The major constraint was that the average overall estimated breeding value (EBV) should be the same as the observed one, for not decreasing short-term genetic gain. Optimizing breeding allocations to boars would have led one to decrease coancestry and inbreeding coefficients by approximately 20%. This decrease would have even increased to approximately 30%, would have replacements and disposals been optimized after accounting for genetic variability, keeping the same constraint of genetic level identical to the observed one. These results showed the potential value, in the future, of completing each periodical calculation of EBVs by optimizations considering genetic variability and of releasing corresponding information to breeders, in order to enhance maintenance of genetic variability.
culled correspondingly. The objective of this paper was to present an optimization strategy for both steps and then to test it in retrospect on actual data. The test population was chosen to be the whole French Landrace population, collectively managed by breeding organizations. The French Landrace population has succeeded in eliminating genotypes sensitive to halothane in the 1980s (Kalweit 1985) and in improving prolificacy since the early 1990s, first by spotting hyperprolific boars and spreading them into the population (Legault 1988), then by putting a high weight on prolificacy (~40% until 2002, and ~25% since 2002) in the selection objective of the population (Tribout et al. 1998). Understandably, inbreeding rate was intense, 0.35% per year, over the period 2000–2004 (Delaunay & Mourg 2006) and even more before (Maignel et al. 1998; Maignel & Labroue 2001).

The population on which the proposed method was tested included 2520 sows located in 26 selection herds, between 15 September 2002 and 9 February 2003. Given the corresponding observed matings, the test in retrospect intended to assess whether substantial decrease of inbreeding and coancestry would have been allowed by the method while keeping the genetic gain for the overall estimated breeding value (EBV) at its observed value.

**Material and methods**

*Optimizing service*

At the moment when service was to be optimized, identification of females to be bred and identification of available males, candidates for service were known with certainty. Selection of females was not carried out in this step. Males were either artificial insemination (AI) or natural service (NS). For simplicity, this last category also included private boars exploited via insemination in a single herd. Consequently, AI meant using a boar located in an AI centre and accessible to all of the 26 herds. Optimization was stepwise, as in the general approach recommended by Sonesson & Meuwissen (2002): first, the number of sows to be served by each selected boar was calculated so as to decrease long term inbreeding rate, then the best matings were determined so as to decrease short term inbreeding.

*The biological model used*

The test period was 21 weeks long, corresponding approximately to the time needed for breeding once (except for return) all of the active breeding females in the population. However, during this period, available males were not always the same and moreover, EBV for males varied depending on the monthly evaluation. In order to take this fact into account in the simulation, the test period was subdivided into five sub-periods of approximately 1 month (the periodicity of evaluation), considering that this choice was an acceptable trade-off between accuracy and complexity.

*The optimization criterion*

At a given sub-period, the ultimate objective was to minimize the average pairwise coancestry coefficient in the population of sows and of the selected boars, considering also the recommendations, hence gestations initiated, in the previous sub-periods of the test period. Then, management of males was not only within sub-period but also between sub-periods.

*Calculating breeding allocations of males*

Calculating the optimized breeding allocations of boars accounted for several very different constraints, moreover established for each sub-period. As the major constraint, the desired average EBV for males after weighing by breeding allocations was fixed. Besides, desired AI rates (here, the observed ones) were fixed for each of the herds, because AI rates depended very much on herds.

The general system of equations to be solved was described by Meuwissen (1997) and Colleau et al. (2004b). The present implementation is described in Appendix 1. First, previous recommendations of males, identifications of the females up to the current sub-period, possible single NS candidates in their herds for the current sub-period, were accounted for in the right hand side of the system, where current constraints were included too. As in these authors, the optimization method solved a series of linear systems of decreasing size where negative solutions for breeding allocations were set to 0 before the next run. As mentioned by Pong-Wong & Woollams (2007), this method is quite simple but is not insured to find the true optimum. Due to the small numbers of males involved, solution of linear systems was obtained by direct inversion. If this process generated selected NS males with no NS contemporary males in their herds, then the size of the linear system to be solved and its e right-hand side s were modified accordingly.

*Optimizing matings*

Matings had to be organized so that inbreeding of progeny would be minimal, given that matings of
NS sires outside their herds were forbidden and that for each herd, a specific average EBV for sires was desired. Values for these constraints were the observed ones. The optimization method was simulated annealing (Kirkpatrick et al. 1983; Robert & Casella 1999; Sonesson & Meuwissen 2000, 2002), implemented twice and stepwise. Annealing 1 had to provide for each herd using AI, the list of AI sires and the corresponding number of sows. Using as herd constraints the number of sows bred by AI and the desired average EBV for the corresponding sires (function of the desired average EBV per herd and of the average EBV of selected NS sires per herd), simulated annealing tried to minimize the average absolute difference, over herds, between desired herd averages for sire EBV and observed herd averages. The observed averages depended on simulated configurations, obtained first by generating a random mating design and then permuting sires currently allocated to two sows chosen randomly.

Annealing 2 consisted of separate within-herd optimizations because for each herd, the sires to be used and corresponding breeding allocations were completely determined.

**Combined optimization of replacement, disposal and service**

Replacement consists of choosing the best animals entering breeding career and disposal concerns the most appropriate animals leaving out breeding, especially females. For instance, females with a least one farrowing (old females) bred in crossbreeding were introduced as extra available candidates because their exclusion from pure breeding might have been a wrong decision. In contrast, old females not bred at all during the test period were not re-introduced because this culling decision might have serious biological reasons.

Optimizing replacement consisted of selecting young animals evaluated for the first time based on their performances on farm and selecting available breeding animals for a further use. Then, both categories competed for breeding.

Establishing the corresponding ranking would not have been enough. A correct management of genetic variability required that optimal breeding allocations for young males would be known, primarily to know whether a young male should have been directed towards AI or towards NS.

The first genetic evaluation and the selection of the young male and female candidates occurred at 5 months of age, whereas age at first breeding occurred at 8 months for females and NS males, and at 10 months for AI males due to sanitary requirements. For the posterior simulation, we assumed that the selection of the young candidates was postponed for 3 months and occurred just before their first possible mating. In this way, all young candidates (actually selected and culled ones) were competing with the contemporary competitors already available. Because evaluations occurred monthly in this population, the evaluations considered in the optimization were the evaluations immediately following the targeted age.

As a result of this simulation procedure, candidates at a given sub-period mixed individuals available at this sub-period and young individuals culled 3 months earlier when they were 5-month-old. Then, for each sub-period, males were the same as the male candidates (either AI or NS) in the optimization of service, plus the young males culled 3 months earlier. Females were the females included in the optimization of service, plus the females used in crossbreeding in this sub-period, plus the young females culled 3 months earlier. The whole procedure is divided into three successive optimizations, the last one corresponding to the optimization for service described previously. Optimization 1 aims at ranking candidates in the whole population, ignoring herd constraints. In optimization 2, females are selected for use in optimization 3 and males are selected to be candidates in optimization 3, after accounting for herd constraints and the information given in optimization 1.

**Optimization 1**

This first optimization aimed at assessing the intrinsic merit (for the future of the population) of each candidate, male or female, young or old, free from its current situation (AI or NS status, herd). Based on this assessment, a list of elite animals could be set up but selection was not carried out in reality for reasons given below. It was postponed to optimization 2 for females, to optimizations 2 and 3 for males. In optimization 1, only inescapable constraints were introduced i.e. the average EBV of selected candidates (after weighting EBV of males by their breeding allocation) and the total number of breeding females needed. For instance, neither the present status of boars nor the numbers of sows needed for each herd were taken into account. Otherwise, males already in NS and sows located in herds with higher average EBV would have been disfavoured. Furthermore, the virtual status for any male became ‘AI’ because potential maximal
breeding allocation was not tied up with a possible current NS status.

The system of equations became much simpler than for optimization of service (Appendix 2). However, this time, contributions of females should have to be calculated for selection purposes. Corresponding results contradicted biology that forced contributions of selected females to be the same. The procedure followed was approximate, since we were not aware of a well-proven optimal procedure for such a case (Appendix 3). It consisted of a succession of runs where a fraction of females was retained (with the same contribution) and another fraction was discarded. At the end of each run, size of the system was decreased and the right-hand side was modified after accounting for recently ‘fixed’ females. First order sub-runs were involved for eliminating females with negative contributions and within these, second order sub-runs solved the current linear system, via the conjugated gradient method (Hestenes & Stiefel 1952; Stoer & Bulirsch 1983; Colleau et al. 2004b), expedited by the ‘indirect method’ for calculating average relationship coefficients (Colleau 2002). Finally, retained females and retained males constituted the ‘elite list’. Ranks within sex were obtained based on the results of the successive procedure (first selected, ..., last selected, last discarded, ..., first discarded) and were transformed into a latent standard normal variate. This variate was related to the synthetic merit of the candidates in the population. The efficiency of the method described in Appendix 3 was tested against a Monte-Carlo procedure, corresponding to a customized simulated annealing, described in Appendix 4.

Optimization 2

This time, the same practical constraints as in the optimization of service were accounted for. First, selection of females within herd was carried out based on the intrinsic merit of females, according to the number needed. Then, we returned back to the issue of selecting males after selection of females. Situations where no further optimization was needed were investigated. The most obvious case concerned NS old sires, present in the list of sires selected by optimization 1 (elite list), but with no other NS male herdmate and no selected young competitor (lonely NS males: herd case NS0). Then, breeding allocations were already known, given the herd constraints. The other case was akin: if no male of a given herd needing NS was in the list of selected sires, then the first male of the herd in the absolute ranking list was kept, then with known allocation (lonely NS male: herd case NS0). These lonely males in this second case could be either old NS males or young males who were given the NS status from now on. Then, in few words, optimization 1 prepared the identification of selected females and of lonely NS selected males, which opened optimization 2.

Given the selected females and the already fixed male contributions, optimization stricto sensu was carried out as for the optimization of service, this time with a mixture of young and old male candidates of the elite list. An operational problem occurred for herd case NS2 where at least two males were present in the elite list. Then, priority was given to AI overall needs by orienting the males with the most important contribution towards AI. As an example, let us take the case of a breeder having to mate 10 females by NS at a given sub-period and having three young males in the elite list, with calculated breeding allocations corresponding to 5, 6 and 30 females. Then, NS was possible with males 1 and 2, whereas male 3 could be oriented towards AI. Finally, the only practical value of optimization 2 was to determine orientation of young selected males: AI versus NS.

Optimization 3

This optimization was conducted as a service step, therefore managing genetic variability within and across sub-periods. However, the origin of candidates to this step was as heterogeneous as the one of candidates to optimization 1. At a given sub-period, females to be served were young females selected 3 months earlier within the 5-month-old females and the selected old females planned to be mated during this sub-period. Candidate males were young males selected 3 months earlier (NS) or 5 months earlier (AI) and available old males. Therefore, the impact of young AI boars selected by the procedure but not by breeders was postponed to sub-periods 3, 4 and 5 only.

It should be pointed out that this phase accounted for any variation of EBVs, either for males or females, between the moment of the selection decision on young animals and the moment of breeding.

Data set

Data originated from 26 selection herds, with a total of 2520 sows during the test period (Table 1). Some herds, also producing crossbreds, were not present throughout because they did not use Landrace boars or Landrace sows in some of the five sub-periods. Average AI rate was 65% with a substantial standard
deviation between herds (approximately 30%), because extremes were 0% and 100% during this test period. The analysis of the EBVs of males used for the matings observed during this period showed a high variation between herds, since the corresponding standard deviation was approximately 15 units. Scale of the official evaluation was such that one genetic standard deviation for the overall objective was 30 units. These findings led us to introduce corresponding herd constraints into the optimizations previously described. Numbers of boars are shown in Table 2. The males (AI or NS) were considered as available during a full sub-period, when in reality they were available during at least half this sub-period (based on entering or culling dates). Availability was declared for boars when they were involved in at least one observed mating. As to AI boars, availability also accounted for crossbreeding matings in the multiplication tier of the population. However, AI boars used only for crossbreeding in the multiplication tier were excluded, because expected to be rejected by breeders of the selection tier: anyway, they would have had difficulties in fulfilling the requirements for genetic gains, given their EBVs. As a result of this declaration procedure, a substantial proportion of available AI boars was not used at all by breeders of the top tier, in contrast with NS boars.

For calculating inbreeding and coancestry coefficients, pedigrees of live animals and available males were traced back according to the ‘indirect method’ (Colleau 2002; Sargolzaei et al. 2005). Based on the pedigree file (46 133 individuals), the equivalent number of generations was 12.9 (minimum 7.3) for females to be served and 13.0 (minimum 9.3) for the available males.

### Results

#### Optimizing service

Table 3 shows that the average observed coancestry coefficients, based on the matings effectively carried out by breeders, laid in the interval 6–9% which can be considered as substantial. The procedure succeeded in decreasing these coefficients by 26% between males and by 17% for the coancestry between males and females. Optimizing matings reduced the average inbreeding coefficient of progeny by 21%, which is valuable given the substantial observed average inbreeding (6.6%).

This improvement was obtained by considerably changing way of using boars, as expected. First, among the 247 boars available, the procedure selected only 83 boars for use, much less than the 175 boars used by breeders: consequently, the maximum allocation for one boar was 160 sows, much more than 102, the observed one. Then, less numerous but more targeted boars were used. Second, the 69 boars used both by the procedure and by breeders corresponded to quite independent allocations ($r$ between both allocations = −0.01).

A dramatical example of the discrepancy between both allocations was given by the most recommended boar by optimization (160 sows). This AI boar, which was available during all the sub-periods was used by breeders on only two sows. This high recommendation rate was mainly due to its low

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**Table 1** Herd characteristics

<table>
<thead>
<tr>
<th>Sub-period</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of sows</td>
<td>373</td>
<td>636</td>
<td>463</td>
<td>491</td>
<td>557</td>
<td>2520</td>
</tr>
<tr>
<td>Number of herds</td>
<td>22</td>
<td>25</td>
<td>25</td>
<td>26</td>
<td>24</td>
<td>26</td>
</tr>
<tr>
<td>AI rate (%)</td>
<td>64 (34)</td>
<td>61 (31)</td>
<td>64 (36)</td>
<td>74 (33)</td>
<td>64 (35)</td>
<td>65 (31)</td>
</tr>
<tr>
<td>EBVs of boars</td>
<td>126 (5)</td>
<td>127 (15)</td>
<td>128 (15)</td>
<td>129 (14)</td>
<td>130 (16)</td>
<td>128 (14)</td>
</tr>
</tbody>
</table>

**Table 2** Numbers of boars for artificial insemination (AI) or natural service (NS)

<table>
<thead>
<tr>
<th>Sub-period</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>AI boars</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In use</td>
<td>45</td>
<td>51</td>
<td>50</td>
<td>45</td>
<td>45</td>
<td>95</td>
</tr>
<tr>
<td>Available</td>
<td>128</td>
<td>129</td>
<td>123</td>
<td>127</td>
<td>131</td>
<td>164</td>
</tr>
<tr>
<td>NS boars</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In use</td>
<td>45</td>
<td>60</td>
<td>53</td>
<td>51</td>
<td>53</td>
<td>80</td>
</tr>
<tr>
<td>Available</td>
<td>49</td>
<td>61</td>
<td>63</td>
<td>63</td>
<td>61</td>
<td>83</td>
</tr>
</tbody>
</table>

**Table 3** Results of optimized service

<table>
<thead>
<tr>
<th>Coancestries (%)</th>
<th>Data</th>
<th>Optimized</th>
<th>Reduction (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male–male</td>
<td>8.55</td>
<td>6.34</td>
<td>26</td>
</tr>
<tr>
<td>Male–female</td>
<td>6.84</td>
<td>5.70</td>
<td>17</td>
</tr>
<tr>
<td>Female–female</td>
<td>6.33</td>
<td>6.33</td>
<td>0</td>
</tr>
<tr>
<td>Inbreeding (%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>6.59</td>
<td>5.20</td>
<td>21</td>
</tr>
<tr>
<td>SD</td>
<td>1.96</td>
<td>2.09</td>
<td></td>
</tr>
</tbody>
</table>
coancestry with male candidates (4.25%) and females (3.75%), whereas his EBV was only slightly higher than the average EBV of male candidates (123 versus 122.1).

The impact of optimization was much higher on matings with AI boars than on matings with NS boars. In the first case, the average inbreeding coefficient was 4.70%, i.e. substantially lower than the observed value (6.50%). In the second case, the average inbreeding coefficient was 6.10%, i.e. slightly lower than the observed value (6.76%).

As a first reason, the previous data set statistics showed that the possible selection intensity between NS candidates was much lower than between AI candidates. Furthermore, it turned out that NS candidates were much more related with their herdmate females than AI candidates: the average coancestry coefficients were 8.44 and 6.83%, respectively. Then, higher inbreeding coefficients from NS boars were expected, despite the optimization.

All of NS boars were sons of AI boars. Then, their coancestry with AI candidates (7.11%) was almost as high as the average coancestry between AI candidates (7.99%). Consequently, the higher coancestry of NS candidates with their herdmates was mainly due to coancestry by female ancestors, as a consequence of the fact that generally, in the French pig selected populations, NS boars were operating in their birth herd (very few exchanges of live boars). The average optimized coancestry coefficient between females and selected boars increased steadily, as expected, when the number of sub-periods considered accumulated. Corresponding values were 5.29, 5.46, 5.58, 5.72 and 5.70%. Corresponding average coancestries between selected males did not exhibit this trend (6.52, 6.46, 6.39, 6.47 and 6.34%). The lack of clear increase was probably due to the fact that the set of candidates was not constant throughout the whole period.

Combined optimization of replacement, disposal and service

The procedure used for optimization 1 was found to be satisfactorily efficient. At the first sub-period (average coancestry between candidates: 6.75%), the single one where this comparison was carried out, the average coancestry coefficient between selected animals was found to be 4.95% by simulated annealing, whereas the much faster analytic procedure led to an average coefficient of 4.97%, slightly higher.

Table 4 shows that the combined optimization led to an additional decrease of coancestry, as compared with optimization of service only. The extra decreases were 11, 15 and 14% for the coancestries male-male, male-female, female-female, respectively. Inbreeding resulting from the corresponding matings was additionally decreased by 11%, so that the inbreeding coefficient was much lower (4.4%) than the observed one (6.6%).

Tables 5 and 6 show that this favourable result was mainly achieved through changing age of selected breeding animals, obtained after optimization 2 for females and after optimization 3 for males. Less than half (43%) of the females used by breeders

### Table 4 Results of combined optimization

<table>
<thead>
<tr>
<th>Coancestries (%)</th>
<th>Data</th>
<th>Optimized</th>
<th>Reduction (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male–male</td>
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</tr>
<tr>
<td>Male–female</td>
<td>6.84</td>
<td>4.65</td>
<td>32</td>
</tr>
<tr>
<td>Female–female</td>
<td>6.33</td>
<td>5.46</td>
<td>14</td>
</tr>
<tr>
<td>Average</td>
<td>7.14</td>
<td>5.03</td>
<td>30</td>
</tr>
<tr>
<td>Inbreeding (%)</td>
<td>6.59</td>
<td>4.40</td>
<td>32</td>
</tr>
</tbody>
</table>

### Table 5 Origin of females in the combined procedure

<table>
<thead>
<tr>
<th>Origin</th>
<th>Candidates in optimization 1</th>
<th>Selected after optimization 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young</td>
<td>813</td>
<td>321</td>
</tr>
<tr>
<td>Used in pure breeding</td>
<td>445</td>
<td>35</td>
</tr>
<tr>
<td>Used in crossbreeding</td>
<td>7358</td>
<td>1272</td>
</tr>
<tr>
<td>Total</td>
<td>8616</td>
<td>1628</td>
</tr>
<tr>
<td>Old</td>
<td>1707</td>
<td>609</td>
</tr>
<tr>
<td>Used in pure breeding</td>
<td>1317</td>
<td>283</td>
</tr>
<tr>
<td>Used in crossbreeding</td>
<td>3124</td>
<td>892</td>
</tr>
<tr>
<td>Total</td>
<td>11740</td>
<td>2520</td>
</tr>
</tbody>
</table>

### Table 6 Origin of males in the combined procedure

<table>
<thead>
<tr>
<th>Origin</th>
<th>Candidates in optimization 1</th>
<th>Selected after optimization 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Young</td>
<td>39</td>
<td>2</td>
</tr>
<tr>
<td>Available for AI</td>
<td>21</td>
<td>3</td>
</tr>
<tr>
<td>Available for NS</td>
<td>3966</td>
<td>53</td>
</tr>
<tr>
<td>Total</td>
<td>4026</td>
<td>58</td>
</tr>
<tr>
<td>Old</td>
<td>125</td>
<td>14</td>
</tr>
<tr>
<td>Available for AI</td>
<td>62</td>
<td>17</td>
</tr>
<tr>
<td>Available for NS</td>
<td>189</td>
<td>31</td>
</tr>
<tr>
<td>Total</td>
<td>4115</td>
<td>89</td>
</tr>
</tbody>
</table>
were present in the optimized list (Table 5). Age distribution changed very much because fraction of young females increased from 32% to 59%: approximately 4 of 5 of these young optimized females were culled by breeders, thus illustrating the need for an efficient replacement system. Furthermore, approximately one-third of the selected old females were not used in pure breeding by breeders, illustrating also the need for a more efficient culling system. In the actual population, the 2520 sows originated from 1865 litters and in the optimized one, from only 1465 litters. Furthermore, only 882 litters were common to both populations. Concerning males, 30% of the real male candidates for service were young males (Table 6). This proportion jumped to 65% after implementing the procedure, reflecting a phenomenon analogous to the one observed for females. Dramatically enough, 53 boars (either AI or NS) out of the 89 recommended were young boars culled by breeders.

Quite clearly, the optimization procedure did its best to find new sources of variability in the numerous young populations previously culled and utilized them. Then, the modification induced was quite strong. This phenomenon would not be likely to continue, if the old females would be preselected by the procedure, as a result of its routine implementation. Then, the value of old female competitors would be better and age distribution would be expected to return to the normal one.

Discussion and conclusion

The perspective of optimization was the same as in the approach tested by Colleau et al. (2004a) for dairy cattle, i.e. minimizing coancestry rate while maintaining the expected genetic gain, based on current EBVs of candidates, to a desired value. The reason invoked for this option, in contrast with the generally recommended option where the expected genetic gain was maximized for desired inbreeding rate, was that breeders are not still familiar with inbreeding coefficients, and even less with inbreeding rates. It was considered here that the same argument held for pig breeders and that in a breeding competition context, even stronger than for dairy cattle, they would unavoidably modulate constraints for inbreeding rates so as to yield a range of acceptable rates of genetic gains. For the present study in retrospect, genetic gains were the observed ones and the short term purpose was to show to breeders that their breeding schemes could be as efficient as usual, while yielding less nuisances. For the long term however, it has to be recognized that breeders will be forced to decrease gradually their desired genetic gains to keep with reasonable inbreeding and coancestry rates. In such a circumstance, switching the constraint might be envisioned.

Despite the fact that optimization procedures used for the test in retrospect were not strictly optimal, from a mathematical view point, this test clearly showed that a substantial amount of coancestry and inbreeding could have been avoided, without sacrificing any genetic gain. The order of magnitude (20–30%) was in accordance with the one found for investigations in retrospect on cattle (Kearney et al. 2004; Colleau et al. 2004b).

In the test in retrospect, all needed information was available. If this procedure were implemented in practice, with a high frequency (each month or ideally each week to fit with the pace of selection and mating decisions within herds), the major hurdle would not be computation time (here, approximately 5 min CPU per sub-period, i.e. for each additional evaluation) but fast transmission by breeders of identification of females to be mated after the next evaluation and of available males. Given the importance of controlling efficiently increases of coancestry and inbreeding, this objective is planned to be achieved by collective French pig populations. Meanwhile, in France, average coancestries of breeding animals with the population have been given to breeders and over-exploitation of some boars has been clearly discouraged (Delaunay & Merour 2006). The next logical step towards the genuine optimization would be to introduce a penalized EBV, a step already implemented in the Swiss pig population (Luther & Hofer 2006). However, it should be recognized that this method is only sub-optimal. For instance, based on optimization 1 of the combined procedure, only 50–60% of the variation of ranks in the candidate population could be predicted by a linear function combining EBV and both coancestries (with candidates of the same sex or with candidates of the other sex).

References


Appendix 1

Optimizing service

This appendix shows how contributions of boars at a given sub-period are obtained, given the previous contributions of the boars used during the previous sub-periods and given the possible cases of lonely selected NS boars in some herds.

At a given sub-period \( j \), the number of selected sows up to this sub-period included, is \( N \). Then, the vector of contributions of females is \( \mathbf{x}_1 = 0.5N^{-1}\mathbf{1}_N \). The vector of relative contributions of the \( M \) male candidates up to sub-period \( j \) included is \( \mathbf{x}_2 \) such that \( \mathbf{1}'_M \mathbf{x}_2 = 0.5 \). Only \( M_V \) males are competing for the current sub-period and \( M_V = M - M_C \) males are no longer competing, with known contributions \( \mathbf{x}_{2V} \). These males also include the lonely NS boars for the current sub-period because their current contributions are already known given the herd constraints for AI rate. Vector of corresponding contributions is \( \mathbf{x}_{2F} \). The current male candidates have known past contributions \( \mathbf{x}^2_{2V} \), up to period \( j - 1 \) included, and current contributions \( \mathbf{x}_{2V} \). The total contribution of the \( N_I \) females of sub-period \( j \) is \( 0.5N_I/N \). Total contribution of males for this sub-period should be the same. Then, the first constraint for \( \mathbf{x}_{2V} \) is \( \mathbf{1}'_M \mathbf{x}_{2V} = C_V = 0.5N_I/N - \mathbf{1}'_M \mathbf{x}_{2F} \). Vectors of EBVs for fixed and unfixed males at the current sub-period are \( \mathbf{b}_F, \mathbf{b}_V \) of dimensions \( M_F, M_V \) respectively. \( B \) is the average EBV weighted by current contributions, required for the sub-period considered and \( B_V \) is the required average EBV for unfixed current contributions, then \( \mathbf{b}'_F \mathbf{x}_{2V} = B_V = 0.5B \mathbf{N}_I/N - \mathbf{b}'_F \mathbf{x}_{2F} \). The current unfixed candidates are linked by incidence.
matrix $H_v$, with $t$ columns, to $h$ herds where some NS is required and where at least two males are competing for NS. Vector of corresponding constraints is vector $s$, of dimension $t$. If herd $k$ requires $N_k$ sows to be mated to NS boars, then $s_k = 0.5N_k/N$. The objective of the optimization is to minimize the average coancestry between breeding animals, i.e. $\frac{1}{2}x^TAx$ where $A$ is the whole relationship matrix between the $N + M$ animals. Sub-matrices for females and males are $A_{11}$, $A_{22}$ respectively. Sub-matrix females-males is $A_{12}$. The Lagrange function is

$$0.5x'Ax + \lambda_1(1_{M_t}x_{2V} - C_{2V}) + \lambda_2(b_{0V}x_{2V} - b_{2V}) + \theta'(H_v - s)$$

where the greek symbols refer to the Lagrange multipliers pertaining to constraints. The system to be solved is:

$$\begin{pmatrix} A_{2V,2V} & 1_{M_t} & b_{0V} & H_v \\ 1_{M_t} & 0 & 0 & 0 \\ b_{2V} & 0 & 0 & 0 \\ H_v & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} x_{2V} \\ \lambda_1 \\ \lambda_2 \\ \theta \end{pmatrix} = \begin{pmatrix} D_v \\ C_v \\ B_v \end{pmatrix}$$

where $-D_v = A_{2V,1V}x_1 + A_{2V,2F}x_{2F} + A_{2V,2V}x_{2V}$. Here, it should be recalled that fixed contributions are not accounted for through corresponding constraints but through modifications of the right hand side of the system only including the ‘variable’ contributions. Over runs, negative solutions lead one to reduce length and composition of vector $x_{2V}$ until each term is positive. Furthermore, additional NS boars can become fixed, if it turns out they remain lonely with positive contributions, and then, matrix $H_v$ is updated.

Appendix 2

Optimization 1 for replacement and disposal

This appendix details the algorithms involved when jointly optimizing replacement and disposal, given the minimal constraints (average EBV of progeny and number of selected females).

At a given sub-period $j$, the number of sows to be selected is $N_j$. The number of sows already selected at the previous sub-periods is $N_P$. The vector of contributions for the latter females is $x_{1F} = 0.51_{N_j}/N$ where $N = N_j + N_P$. For the male candidates in the previous sub-periods who are no longer candidate in the current sub-period, vector of previous contributions is $x_{2F}$. For the $M_V$ males competing in the current sub-period, vector of current contributions is $x_{2V}$, and vector of previous contributions is $x_{2V}$. Then, the first constraint for $x_{1V}$ is $1_{N_F}x_{1V} = C_V = 0.5N_j/N - 1_{N_F}x_{1F}$ and the first constraint for $x_{2V}$ is $1_{M_t}x_{2V} = C_V$. $B$ is the average estimated breeding value requested for the progeny born from the current matings. Then, $b_{0V}x_{1V} + b_{2V}x_{2V} = 0.5BN_j/N = B_v$. The Lagrange function is

$$0.5x'Ax + \lambda_1(1_{N_F}x_{1V} - C_V) + \lambda_2(1_{M_t}x_{2V} - C_V) + \lambda_3(b_{0V}x_{1V} + b_{2V}x_{2V} - B_V).$$

The system to be solved is:

$$\begin{pmatrix} A_{1V,1V} & A_{1V,2V} & 1_{N_F} & 0 & b_{1V} \\ A_{2V,1V} & A_{2V,2V} & 0 & 1_{M_t} & b_{2V} \\ 1_{N_F} & 0 & 0 & 0 & 0 \\ 0 & 1_{M_t} & 0 & 0 & 0 \\ b_{1V} & b_{2V} & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} x_{1V} \\ x_{2V} \\ \lambda_1 \\ \lambda_2 \\ \lambda_3 \end{pmatrix} = \begin{pmatrix} D_{1V} \\ D_{2V} \\ C_V \\ C_V \\ B_V \end{pmatrix}$$

where $-D_{1V} = A_{1V,1F}x_{1F} + A_{1V,2F}x_{2F} + A_{1V,2V}x_{2V}$ and $-D_{2V} = A_{2V,1F}x_{1F} + A_{2V,2F}x_{2F} + A_{2V,2V}x_{2V}$. Successive fixations of current females to contributions $0.5/N$ and eliminations leads one to increase $N_F$.

Appendix 3

Ranking procedure based on successive runs of optimization

This procedure aims at decreasing progressively the size of the system to be solved due to selecting at each run some females and discarding some males and females, until the fate of each candidate is fully determined. Number of runs is $t$ (at any sub-period, a value of 20 is enough). Therefore, $t$ major linear systems are solved, within which minor steps are carried out for setting solutions to 0.

At the end of each major run, individuals still in competition in the current system are classified within sex: individuals sorted by decreasing contributions, individuals with 0 contributions sorted from late to early elimination. Then, the $N_{M_0}/t$ best females are fixed and the $0.3(N_V - N_j)/t$ worst females, the $0.5M_0/t$ worst males are dropped out for further runs. Consequently, elimination is not too brutal to avoid losing candidates still valuable for further runs.

The eventual ranking of females is as follows:

Fixed at run 1, ..., fixed at run $t$, eliminated at run $t$, ... eliminated at run 1.

The eventual ranking of males is as follows:

By decreasing contribution at run $t$, eliminated at run $t$, ... eliminated at run 1.
Appendix 4

Simulated annealing for finding solutions of optimization 1 (replacement and disposal)
The analytical procedure of Appendix 3 is only approximate. Appendix 4 presents a Monte-Carlo, simulated annealing-based, method, likely to yield better performances.

In some circumstances, such as optimizing matings given contributions, simulated annealing is easy to implement, because permutations are enough for generating alternatives. Here, the permutation principle was kept for selecting females. However, alternative solutions should be obtained from unknown number of selected males with unknown contributions, given the constraints for total contributions of males and average breeding value of progeny. For simplicity, the following procedure was tested in sub-period 1.

Generating an initial solution
Select the N females with estimated breeding values close to B, the value required for progeny.

Do the same for 100 males and set equal contributions.

Add one male and modify contributions so that the B constraint is exactly met.

The procedure of addition is the same as below.

Generating an alternative solution
(i) Permute a selected female, chosen randomly and an unselected female, chosen randomly.

Then, for the B constraint to be met, the weighted average of selected males should change from $B_2$ to $B_2 + AB_2$. With equal probability 0.1, one male is added or removed with modifications of contributions, with the rule that relative contributions of the other selected males remain unchanged. With probability 0.8, internal modifications of contributions for the current list of selected males are carried out. These modifications only affect a pair of individuals.

The optimal probabilities are determined a posteriori by running simulated annealing at the initial temperature and by testing nine situations. In situation $i$, probabilities of addition, removal, internal modification are $0.5(1 - i/10)$, $0.5(1 - i/10)$, $i/10$ respectively.

(ii) Add one male (probability 1/10).

If $AB_2$ is positive, chose randomly an unselected male such that his EBV $b$ is larger than $B_2 + AB_2$. Then, contribution $x$ of this individual is $x = 0.5AB_2/(b - B_2)$. Contributions of initial males are multiplied by $1 - 2x$.

If $AB_2$ is negative, chose randomly an unselected male such that his EBV $b$ is smaller than $B_2 - AB_2$. Then, contribution $x$ of this individual is $x = 0.5AB_2/(b - B_2)$. Contributions of initial males are multiplied by $1 - 2x$.

(iii) Or remove one male (probability 1/10).

This removal is carried out in two steps.

In the first step, one chooses the male i such that the new weighted average for EBV is the closest to the required average, i.e. $B_2 + AB_2$. If a male with EBV equal to $b$ and contribution $x$ is removed, then the new average EBV becomes $(B_2 - 2bx)/(1 - 2x)$. Contributions of unaffected individuals are updated accordingly, i.e. divided by $1 - 2x$.

In the second step, calculate for each remaining selected male the quantity $x^* = [(0.5 - x)(b_1 + AB_2)]/\left((b - 2\sum b_i x_i)\right)$, where $x$ is the updated contribution. Choose randomly one male $j$ such that $x^*_j$, his new contribution, lies between 0 and 1. Contributions of the other selected males are obtained after multiplying the current ones by the ratio $(1 - 2x^*_j)/(1 - 2x_j)$.

(iv) Or modify contributions of a pair of males (probability 8/10).

Chose randomly a male $i$. If the constraints can still be met after manipulating contributions of this male and of another male $j$, then $\Delta x_i \leq 0.5$. Feasibility conditions are $0 \leq x_i + \Delta x_i \leq 0.5$ and $0 \leq x_j - \Delta x_j \leq 0.5$. If no $j$ is feasible within five attempts corresponding to five different $i$ chosen randomly, then give up.