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Original article

Modelling and optimizing of sequential selection schemes: a poultry breeding application

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Summary – A sequential selection scheme, where candidates are ranked using a multiple trait BLUP selection index, was modelled deterministically. This model accounts for overlapping generations and for the reduction of genetic variances under selection, in order to predict the asymptotic genetic gain. Sires and dams are selected among the pairs already created whose progeny have maximum expected average genetic merit. This procedure allows for an optimal use of the available information when the pairs are selected. Effects of selection on the mean and variance of the traits measured on selected animals are accounted for using the Tallis formulae, while a matrix formula is used in order to simultaneously derive genetic lags and gains. The evolution of inbreeding rate was not modelled. Numerical applications were related to a turkey breeding plan. The impact of the relative weight given to growth (male and female body weight, measured at 12 and 16 weeks) and reproduction traits (three partial egg number records) on the expected genetic gains was investigated. Influence of demographic parameters was also studied. Different selection strategies were compared. When the selection objective is mainly to improve laying ability, it is more relevant to increase the amount of information on laying performance, and to apply selection of best mated pairs, rather than to reduce generation intervals by only using the youngest sires. This modelling can be viewed as a useful tool, in order to foresee the consequences of any change in the breeding plan for the long-term genetic gain.

genetic gain / deterministic modelling / sequential selection / Bulmer effect / poultry selection

Résumé – Modélisation déterministe et optimisation d'un schéma de sélection séquentiel : exemple d'un schéma « volaille de chair ». *Un schéma de sélection, séquentiel, où les animaux sont classés à l'aide d'un indice BLUP multicaractère a été modélisé. Les générations sont chevauchantes, et la réduction des variances génétiques sous*

* Correspondence and reprints

l'effet de la sélection est pris en compte, afin de prédire le progrès génétique asymptotique. Les reproducteurs choisis sont ceux dont la descendance a, en espérance, la plus forte valeur génétique additive (sélection des meilleurs couples parmi tous ceux déjà formés). Cette procédure permet l'utilisation optimale de l'information recueillie au moment du choix des reproducteurs. Les effets de la sélection sur la moyenne et la variance des caractères sont pris en compte par les formules de Tallis, tandis qu'une formule matricielle est utilisée afin de calculer simultanément le progrès génétique et les écarts de niveau entre cohortes. Les applications numériques portent sur un schéma « dinde » et étudient l'influence de la pondération relative donnée au poids et à la ponte dans l'objectif de sélection sur le progrès génétique attendu pour les sept caractères inclus dans l'objectif (poids mâles et femelles mesurés à 12 et 16 semaines, et trois pontes partielles), et des paramètres démographiques du schéma. Différentes stratégies de sélection sont ainsi comparées. Quand les caractères de ponte sont prépondérants dans l'objectif de sélection, il est préférable d'augmenter le nombre de femelles mesurées en ponte, et de pratiquer une sélection des couples, plutôt que de chercher à réduire l'intervalle de génération en n'utilisant que les plus jeunes mâles. Cette modélisation constitue, malgré l'absence de prise en compte de la consanguinité, un outil utile pour le sélectionneur, afin de prévoir les conséquences, à long terme, de sa politique de sélection.

progrès génétique / modélisation déterministe / sélection séquentielle / effet Bulmer / sélection des volailles

INTRODUCTION

In meat-type poultry populations, efficient evaluation of breeding stocks and effective breeding plans are needed to accomplish the selection objective which, in female strains, is mainly to improve both growth and reproductive ability.

Since the records required to compute a single selection index are not available simultaneously and/or their cost is not compatible with their collection for all the candidates (especially for laying traits), a typical selection scheme involves different stages that correspond to successive truncations on the joint distribution of successive indices. Therefore, in meat-type poultry breeding plans, birds are sequentially measured, evaluated and culled.

The mathematical description of independent culling level selection was presented by Cochran (1951) for two-stage selection and was extended by Tallis (1961) to n stages. Generally speaking, the calculation of genetic gains involves the computation of expected breeding values of selected animals after truncation on the joint normal distribution of estimated breeding values for all the candidates. Maximizing selection response with respect to the truncation points was also considered by Cotterill and James (1981) and Smith and Quaas (1982), but numerical applications were initially limited by very restrictive conditions such as two-stage selection, uncorrelated traits and/or very simple optimization criteria. As proposed by Ducrocq (1984) and Ducrocq and Colleau (1986, 1989), the use of the Dutt method (Dutt, 1973) to compute the Tallis formulae (1961) allows the extension to a larger number of traits and selection stages.

In meat-type poultry female strains, the estimation of genetic merit for reproductive ability is often critical, as reproductive traits are only measured on a restricted fraction of the initial population. To improve selection on laying traits by using individual (and not only pedigree) information on those traits, it may be worthwhile

to perform selection of the best mated pairs, once individual laying performances are recorded, and eggs are already laid.

In this paper, a deterministic approach for predicting the asymptotic genetic gain and lags in a multistage poultry breeding plan is described. It involves selection of best pairs of mated animals with overlapping generations and BLUP evaluation of candidates. The reduction of genetic variances under selection is also accounted for. A turkey breeding plan is considered here but extension to other species is straightforward.

MATERIALS AND METHODS

The breeding plan will first be described in terms of its demographic parameters. Then a probabilistic formulation will be given, in order to compute the truncation thresholds, the genetic selection differentials and the asymptotic expected genetic gain.

Selection procedure

This section will describe the selection procedure (fig 1). The goal of the selection scheme is to obtain hatched chicks with the highest aggregate genotype. Here, the breeding objective considered includes body weight measured at 12 and 16 weeks of age ($BW12$ and $BW16$), and three successive egg production partial records (EN_1, EN_2, and EN_3). In order to account for the sexual dimorphism observed in turkeys, it was decided to consider weights as sex-limited traits (Chapuis et al, 1996). As a consequence, four growth traits were analyzed ($BW12_{♀}$, $BW12_{♂}$, $BW16_{♀}$, $BW16_{♂}$). A total of seven traits was included in the model.

In a given flock, F_n, chicks are sequentially measured, ranked and culled. At each stage of the selection scheme, the ranking of candidates is based on the linear combination of the estimated breeding values for each trait of interest that maximizes the correlation with the overall aggregate genotype. The evaluation uses multiple trait BLUP methodology applied to an animal model, and all data from related animals are used (from ancestors, including their laying performances when available, as well as from sibs used for multiplication).

At the end of the rearing period (t_1), selected birds are considered as potential parents, ie, all the females retained at this stage will be mated and will have their egg production recorded.

The individual information used for this first evaluation includes the 12- and 16-week body weights. No individual performance on egg production is available when these potential parents are selected. The predictors used for selection at this stage will be denoted $I_{1♂}$ and $I_{1♀}$, and the truncation thresholds involved $c_{1♂}$ and $c_{1♀}$. No actual culling occurs thereafter: the $N_{♀}$ female candidates selected at step 1 are either used for selection or used in the multiplication chain. In the breeding plan described here, for practical reasons, only a fraction of the layers are inseminated with identified sperm. As a consequence, even if the egg numbers are recorded for all the females, only a subset of these females is actually considered for selection, because the eggs laid outside this sub-population are not pedigreed. Each male is

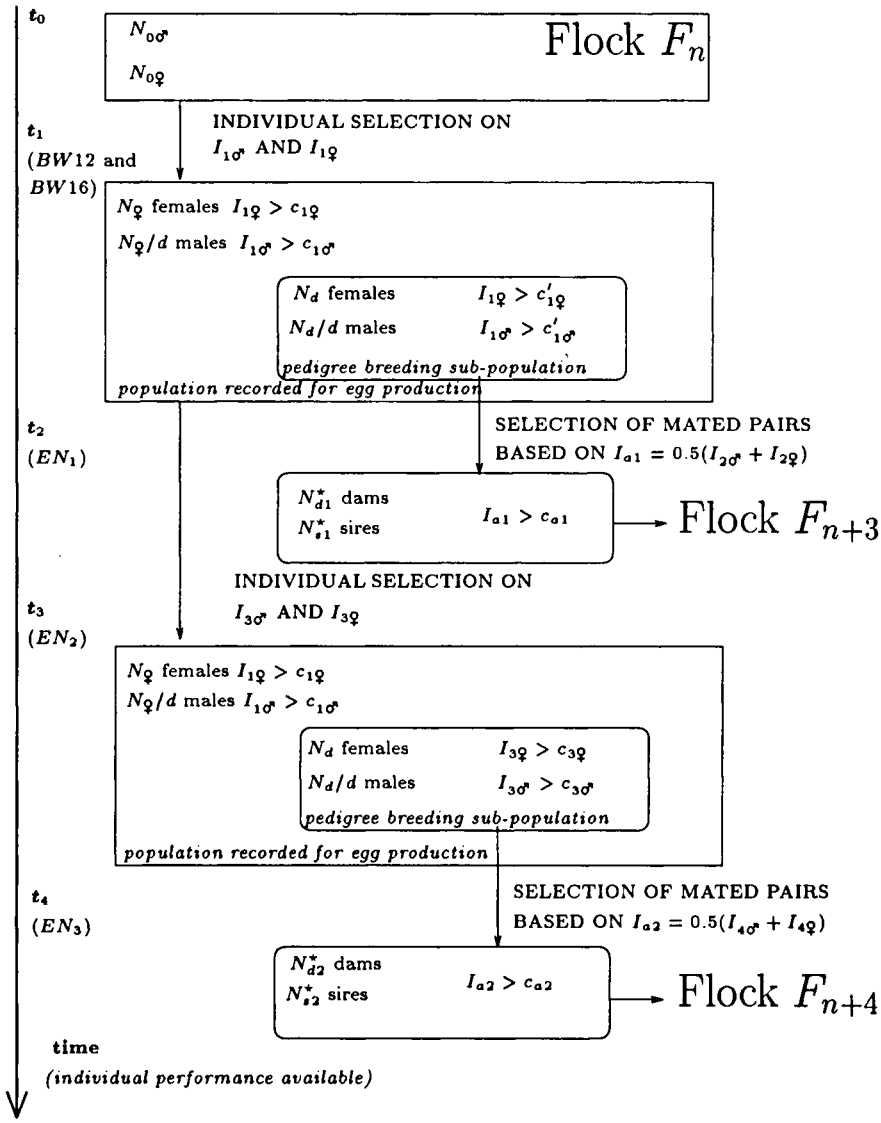

Fig 1. Multi-stage selection procedure of candidates from flock F_n. $BW12$ and $BW16$ indicate body weight measured at 12 and 16 weeks. EN_1, EN_2 and EN_3 indicate successive partial laying performances. d is the number of females mated to each male.

assumed to be mated to d females (N_d females and N_d/d males in total). At t_1, males and females included in this sub-population are characterized by their higher predictor values $I_{1♂}$ and $I_{1♀}$, which are assumed to be above the new truncation thresholds $c'_{1♂}$ and $c'_{1♀}$, respectively higher than $c_{1♂}$ and $c_{1♀}$.

Before being included in the mating design, males are also mass-selected on semen production. This trait is assumed to be uncorrelated with the traits included in the breeding objective and its evolution is not considered here. This selection is accounted for through an adequate (lower) survival rate until the beginning of the egg production recording period.

At t_2, the first individual partial record on egg production EN_1 becomes available. Estimated genetic merits ($I_{2♂}$ and $I_{2♀}$) are then computed, combining previous data with this new information. Pairs in the sub-population previously described are then ranked, based on the expected merit of their progeny ie, on $I_{a1} = 0.5(I_{2♂} + I_{2♀})$. Only eggs with I_{a1} above a threshold c_{a1} will be used to generate F_{n+3}. This is an *a posteriori* selection of best mated pairs, in contrast with a situation where egg production information would be collected before matings are planned among individually selected candidates. This strategy (selection of individuals followed by selection of pairs of parents for eggs already laid) aims at reducing the generation interval, as matings are planned before individual information on egg production is available.

At t_3, 4 weeks before the beginning of the second reproduction period, birds are individually selected including information on EN_2. The lag between t_3 and t_4 ensures that eggs sampled during the second collection are sired by an identified male. Once again this selection allows the constitution of a sub-population of individuals exhibiting the highest values for the estimated aggregate genotype. The predictors used at t_3 are $I_{3♂}$ and $I_{3♀}$. Selected candidates can be the same as in t_1 but this is neither guaranteed nor required. Birds selected at t_1 based on ancestral information can be eliminated from the pool of pedigree breeding candidates if their own performances are lower than expected, leaving room for other candidates. In addition, even if the same individuals are selected again, the mating design may change.

At t_4, the newly created pedigree breeding pairs are ranked using $I_{a2} = 0.5(I_{4♂} + I_{4♀})$. Selected eggs are used to generate F_{n+4}.

Three flocks are successively generated per year. The lag between two flocks depends on the housing facilities and must allow cleaning time for the buildings. This leads to overlapping egg collection periods for two successive flocks (fig 2). Once eggs are selected on their average parent aggregate genotype, they are pooled together. Chicks coming from two parental flocks form a new flock, made up of four cohorts (two male and two female) characterized by their parental origin. For instance, animals in F_{n+4} come from the eggs sampled during the first egg collection of parental flock F_{n+1} ('young' sires and dams) and eggs sampled during the second collection of F_n ('old' sires and dams).

Cohort 1 will hereafter represent females with young parents, cohort 2 females with old parents. Similarly, cohort 3 represents male chicks with young parents and cohort 4 male chicks with old parents. Once a flock is established, birds are reared regardless of their parental origin.

Let $\alpha_♂$ and $\alpha_♀$ be the initial proportions of male and female chicks coming from the first egg collection. Initially, these proportions are assumed to be both fixed and known, so that EBVs of eggs from the two collections are not actually compared when establishing a new flock. Candidates from different cohorts, however, are

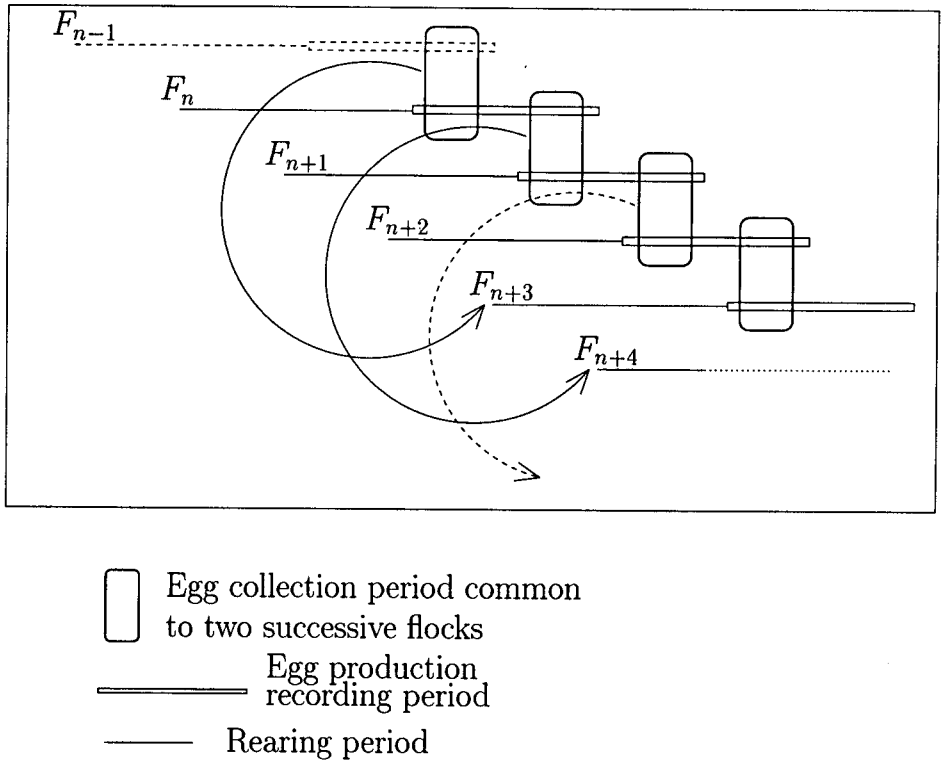

Fig 2. Organization of the different flocks.

compared within a flock, accounting for the differences of mean and variance of their predictors attributable to their distinct parental origins. As fewer males than females are needed for the next generation, the selection intensities applied to the parents of future males and females will differ. Therefore $\alpha_{♂}$ and $\alpha_{♀}$ may be different.

Derivation of truncation thresholds

Two kinds of selection are involved: the first type (later referred to as *individual selection*) is performed on the candidates. The other (*selection of mated pairs*) is performed on their progeny and requires a particular treatment.

Individual selection

This selection occurs at t_1 and t_3. The following notation will be used:

A_{js} represents the event 'a candidate of sex s ($s = ♂, ♀$) is included in the jth pool of pedigree breeding candidates ($j = 1, 2$)';

K_l is the event 'an individual belongs to cohort l ($l = 1, \ldots, 4$)'.

In order to account for the differences of means and variances of the predictors inherent to each cohort, we can write:

$$\text{Prob}(A_{j♀}) = \alpha_{♀}\ \text{Prob}(A_{j♀}|K_1) + (1-\alpha_{♀})\ \text{Prob}(A_{j♀}|K_2)$$

and

$$\text{Prob}(A_{j♂}) = \alpha_{♂}\ \text{Prob}(A_{j♂}|K_3) + (1-\alpha_{♂})\ \text{Prob}(A_{j♂}|K_4)$$

$\text{Prob}(A_{js}|K_l)$ is the result of truncation selection on one (at t_1) or two (at t_1 and t_3) predictors that are assumed to initially have a multivariate normal distribution. $\text{Prob}(A_{js}|K_l)$ is equal to a truncated (possibly multivariate) normal integral, with parameters depending on the cohort considered. To calculate the truncation thresholds, we have to solve several nonlinear equations.

Let $c_{1s}{}^{\star}_{(j)}$ represent the standardized truncation threshold at t_1 for candidates of sex s in cohort j. Let $N_{♀}$ be the number of females measured on reproductive ability, and $N_{0♂}$ and $N_{0♀}$ be the initial numbers of male and female chicks. The S_{is}s are the different survival rates from t_0 to t_i and Φ_j is the standard normal cumulative probability function of dimension j.

Let $Q_{1♂}$ and $Q_{1♀}$ be the fractions of male and female candidates selected at stage 1 to be measured on reproductive ability:

$$Q_{1♀} = \frac{N_{♀}}{N_{0♀}S_{1♀}} \qquad Q_{1♂} = \frac{N_{♀}}{d\,N_{0♂}S_{1♂}}$$

At t_1, the equations to be solved are of the form:

$$Q_{1♀} = \alpha_{♀}\ \Phi_1\left(c_{1♀}{}^{\star}_{(1)}\right) + (1-\alpha_{♀})\ \Phi_1\left(c_{1♀}{}^{\star}_{(2)}\right) \qquad [1]$$

for females and

$$Q_{1♂} = \alpha_{♂}\ \Phi_1\left(c_{1♂}{}^{\star}_{(3)}\right) + (1-\alpha_{♂})\ \Phi_1\left(c_{1♂}{}^{\star}_{(4)}\right) \qquad [2]$$

for males.

Similar equations hold to obtain c'_{1s}, which is the truncation threshold used at t_1 to select candidates of sex s included in the pedigree breeding sub-population: in the latter, replace $c_{1s}{}^{\star}_{(j)}$ by $c'^{\star}_{1s(j)}$ and Q_{1s} by Q'_{1s} where:

$$Q'_{1♀} = \frac{N_d}{N_{0♀}S_{1♀}} \qquad Q'_{1♂} = \frac{N_d}{d\ N_{0♂}S_{1♂}}$$

and N_d is the number of females in the pedigree breeding sub-population.

As shown in figure 3, the standardized thresholds depend on the mean and variance of the predictor in the considered cohort. In a given flock, the thresholds $c_{j♂}$ (or $c_{j♀}$) are common to all classes of chicks of a given sex. This maximizes the expected genetic merit of selected candidates (Cochran, 1951) even when the amount of information available for the evaluation is not equal for all candidates (Goffinet

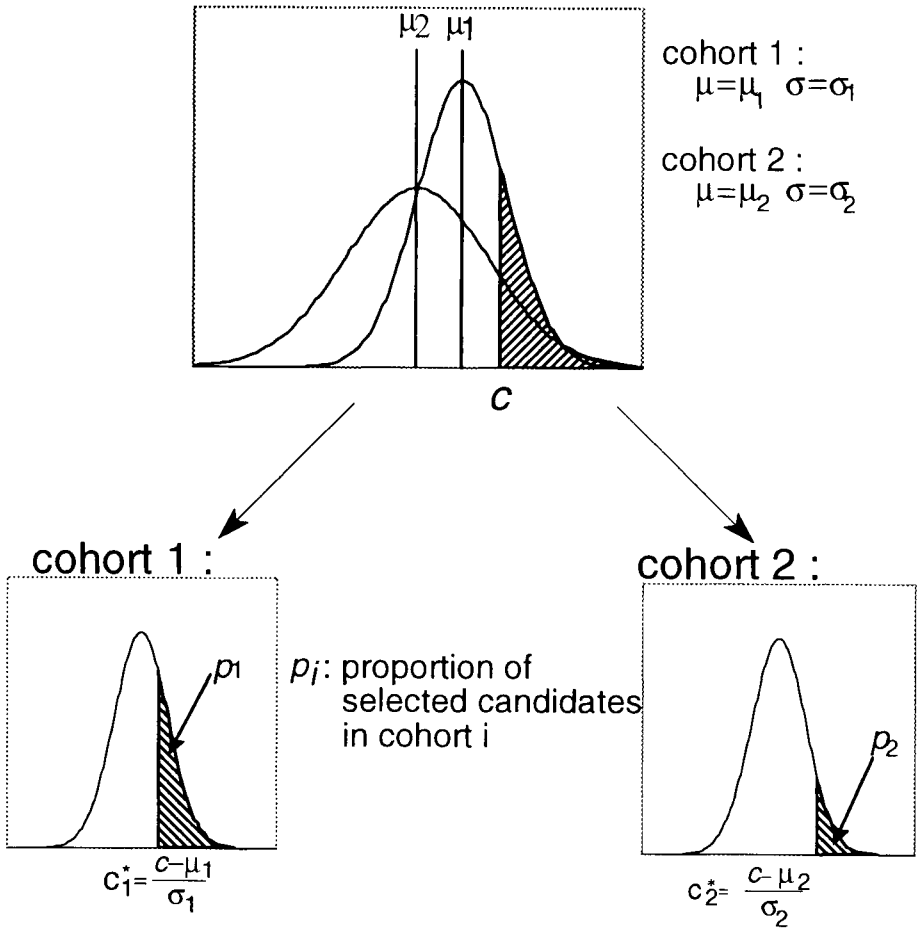

Fig 3. Selection procedure: a common threshold truncation selection is performed on all distributions.

and Elsen, 1984; James, 1987) and simultaneously optimizes the generation intervals and the proportions of different types of parents (James, 1987).

Similarly, let $Q_{3♂}$ and $Q_{3♀}$ be the overall fractions of selected candidates at stage 3

$$Q_{3♀} = \frac{N_d}{N_{0♀} S_{3♀}} \qquad Q_{3♂} = \frac{N_d}{d\, N_{0♂} S_{3♂}}$$

Let $\boldsymbol{R}^{\star}_{s(k)}$ be the correlation matrices of predictors for cohort k (of sex s). At t_3, knowing the previous thresholds $c_{1♂}$ and $c_{1♀}$, the problem is to solve the following

equations in $c_{3♂}{}^{\star}$ and $c_{3♀}{}^{\star}$, where the $c^{\star}$s are the standardized thresholds:

$$Q_{3♀} = \alpha_{♀}\ \Phi_2\left(c_{1♀}{}^{\star}_{(1)}, c_{3♀}{}^{\star}_{(1)}; \boldsymbol{R}^{\star}_{♀(1)}\right) + (1-\alpha_{♀})\ \Phi_2\left(c_{1♀}{}^{\star}_{(2)}, c_{3♀}{}^{\star}_{(2)}; \boldsymbol{R}^{\star}_{♀(2)}\right) \quad [3]$$

and

$$Q_{3♂} = \alpha_{♂}\ \Phi_2\left(c_{1♂}{}^{\star}_{(3)}, c_{3♂}{}^{\star}_{(3)}; \boldsymbol{R}^{\star}_{♂(3)}\right) + (1-\alpha_{♂})\ \Phi_2\left(c_{1♂}{}^{\star}_{(4)}, c_{3♂}{}^{\star}_{(4)}; \boldsymbol{R}^{\star}_{♂(4)}\right) \quad [4]$$

To solve equations [1]–[4] in $c_j^{\star}$ knowing the previous thresholds, and the means and correlations of the predictors, an iterative solution is performed, as proposed by Ducrocq and Quaas (1988), using a Newton–Raphson algorithm.

Selection of mated pairs

This type of selection occurs at t_2 and t_4.

At t_2, $N_d S_1^{\star}$ females (mates) remain candidates to become actual dams of future pedigree chicks. Only $N^{\star}_{d1_s}$ are needed to produce chicks of sex s. We will consider that a young dam produces an equal number of male and female progeny p_y. Thus,

$$N^{\star}_{d1_s} = \frac{\alpha_s N_{0s}}{p_y}$$

The predictor I_{a1} used to select the actual parents at t_2 includes the EBVs of both parents. Let $Q_{2♀_s}$ be the probability of selecting a female at t_2 to give progeny of sex s, *given that the male it was mated with was also previously selected at* t_1. This leads to the equation:

$$\begin{aligned} Q_{2♀_s} &= \text{Prob}\left(I_{♀1} > c'_{♀1}, 0.5(I_{2♀} + I_{2♂}) > c_{a1_s} | I_{1♂} > c'_{1♂}\right) \\ &= \frac{\text{Prob}(I_{♀1} > c'_{♀1}, I_{1♂} > c'_{1♂}, I_{a1} > c_{a1_s})}{\text{Prob}(I_{1♂} > c'_{1♂})} \\ &= \frac{\text{Prob}(B_{1s})}{\text{Prob}(A_{1♂})} \end{aligned}$$

where B_{is} is the event 'a pair is selected at the ith egg collection ($i = 1, 2$) to be 'young' ($i = 1$) or 'old' ($i = 2$) parents of progeny of sex s ($s = ♂, ♀$)', and c_{a1_s} is the truncation threshold used to select chicks of sex s on I_{a1}.

This leads to the equation:

$$\text{Prob}(B_{1s}) = Q_{1♀} \times Q_{1♂} \times \frac{N^{\star}_{d1_s}}{N_d S_1^{\star}} \quad [5]$$

The first term is the fraction of females selected at t_1, the second the fraction of males selected at t_1, and the third is the fraction of mates selected at t_2 among all the pairs already formed.

Males and females are mated regardless of the cohort they originate from, so that we can write:

$$\text{Prob}(B_{1s}) = \sum_{j=1,2} \sum_{k=3,4} \zeta(j)\zeta(k)\Phi_3 \left(c'_1{}^{\star}, c'_1{}^{\star}, c^{\star}_{a1_s}; \boldsymbol{R}^{\star}_{(jk)}\right)$$

$$\zeta(1) = \alpha \ , \ \zeta(2) = 1-\alpha \ , \ \zeta(3) = \alpha \ , \ \zeta(4) = 1-\alpha \qquad [6]$$

For the sake of clarity, the subscripts j and k that refer to the cohorts were dropped in [6] for the thresholds. As in equations [1]–[4], * denotes standardized variables. Again, a Newton–Raphson algorithm is used to solve this nonlinear equation.

Similarly, at t_4, the equation to be solved for $c^{\star}_{a2_s}$ is:

$$\text{Prob}(B_{2s}) = \sum_{j=1,2} \sum_{k=3,4} \zeta(j)\zeta(k)\Phi_5 \left(c_1{}^{\star}, c_3{}^{\star}, c_1{}^{\star}, c_3{}^{\star}, c_{a2_s}{}^{\star}; \boldsymbol{R}^{\star}_{(jk)}\right)$$

$$= Q_3 \times Q_3 \times \frac{N^{\star}_{d2_s}}{N_d S^{\star}_2} \qquad [7]$$

where c_{a2_s} is the truncation threshold pertaining to $I_{a2} = 0.5(I_4 + I_4)$, $N^{\star}_{d2_s}$ depends on p_0, which is the average prolificacy of old dams. Here the third fraction corresponds to the number $(N^{\star}_{d2_s})$ of mating pairs needed to produce progeny of sex s in flock F_{n+4} divided by the number of candidates. $N^{\star}_{d2_s}$ depends on p_0, which is the average prolificacy of old dams.

Genetic gains and lags

Once the different truncation thresholds have been calculated, it is possible to derive the genetic superiority of selected animals, and the asymptotic genetic gain. For this purpose, the probability of selecting a parent (sire or dam) from cohort i to give progeny in cohort j is required.

Proportions of selected parents

Let w_{ij} be the within-sex proportion of parents selected from cohort i to give progeny in cohort j, among all the parents selected to give progeny in cohort j. These proportions are required, as they represent the contribution of each cohort to the genetic gain. To obtain w_{ij}, it is only necessary to sum from the expressions above ([6] for $j = 1,3$ or [7] for $j = 2,4$) the terms in $\zeta(i)$, and to divide the resulting quantity by the overall sum. For example, w_{31} is the proportion of sires from cohort 3 used to give progeny in cohort 1. As there are only two male cohorts, we have $w_{31} + w_{41} = 1$ and

$$w_{31} = \frac{\zeta(3)\sum_{k=1,2}\zeta(k)\boldsymbol{\Phi}_3\left(c'_1{}^{\star}_{(k)}, c'_1{}^{\star}_{(3)}, c_{a1}{}^{\star}_{(k3)}, \boldsymbol{R}^{\star}_{(k3)}\right)}{\text{Prob}(B_1)} \qquad [8]$$

A male is mated with d dams. The probability of selecting a male as an actual sire should account for all the possibilities that can arise, based on the genetic merit of the dams it is mated with.

Let us define a given pair as 'successful' if its progeny are selected. A male will give progeny of sex s that will be considered as a candidate for later selection if it belongs to at least one successful pair at t_2 (or at t_4). The number of occurrences of these events follows a binomial distribution. Thus, exact derivation of the contribution of a given male to the following generation implies the computation of complex integrals involving power functions of multivariate densities. For this reason, as an approximation, it was considered that the number of successful pairs was the same for each male. Let $d^\star$ be the average number, common to each male, of successful pairs.

Genetic selection differentials

Knowing the proportion of selected parents from cohort i to give progeny in cohort j, one can calculate the genetic gain obtained in the overall breeding objective H_1, or in each trait of interest or any linear combination of these (denoted hereafter as H_p, $p = 2, \ldots, r$). For this purpose, we need the expected genetic means of the selected individuals. This is the expectation of H_p, given the truncation thresholds on the predictors I, and assuming a joint multivariate normal distribution of these predictors and H_p. In an n-stage selection procedure, we have:

$$\mathrm{E}(H_p|I_1 > c_1, \ldots, I_n > c_n) = \frac{1}{\mathcal{Q}} \int_{-\infty}^{+\infty} h_p \int_{c_1}^{\infty} \cdots \int_{c_n}^{\infty} \phi_{n+1}(h_p, x_1, \ldots, x_n) \mathrm{d}x_n \ldots \mathrm{d}x_1 \, \mathrm{d}h_p \quad [9]$$

with

$$\mathcal{Q} = \int_{c_1}^{\infty} \cdots \int_{c_n}^{\infty} \phi_n(x_1, \ldots, x_n) \mathrm{d}x_n \ldots \mathrm{d}x_1 \quad [10]$$

The x_s in the integrand represents the predictors, and h_p the breeding objective or any linear combination of traits. $\mathcal{Q}$ is given and represents the overall fraction of candidates selected. Because of successive truncations, the distribution of H_p is not normal. Tallis (1961) and Jain and Amble (1962) derived the expression for the moments of the truncated multivariate normal distribution:

$$\mathrm{E}(H_p) = \frac{\rho_{h_p 1} \; z_1 \; \mathcal{Q}_{n-1,1} + \rho_{h_p 2} \; z_2 \; \mathcal{Q}_{n-1,2} + \cdots + \rho_{h_p n} \; z_n \; \mathcal{Q}_{n-1,n}}{\mathcal{Q}} \quad [11]$$

$\mathcal{Q}_{n-1,i}$ is the joint conditional cumulative probability function of the $(n-1)$ variables I_j ($j = 1, \cdots, n$ and $j \neq i$) given I_i, $\rho_{h_p i}$ is the correlation between H_p and I_i, and z_i is the ordinate of the univariate normal density at c_i ($z_i = \phi(c_i)$).

Let $\mathcal{E}_{ij}^{(p)}$ be the genetic selection differential (for H_p) of candidates selected in cohort i to give progeny in cohort j. As selection of mated pairs is involved in selecting the sires and dams, it is necessary, in order to derive the genetic selection differential of a given parent i, to weight the expectation in [11] with the probability of also selecting the parent of opposite sex l. This leads to the following expression for $\mathcal{E}_{ij}^{(p)}$:

$$\mathcal{E}_{ij}^{(p)} = \sum_l w_{lj} \mathrm{E}(H_p | K_i, K_l, B_{ks}) \qquad [12]$$

where k refers to the egg collection considered, s to the sex of the progeny, and the relevant k and s are uniquely specified given j.

Asymptotic genetic gains and lags

A matrix formulation proposed by Phocas et al (1995) is used to simultaneously derive the genetic gain and the lags at birth between the different cohorts. An arbitrary reference class of mean genetic level $M_1^{(p)}$ is used to define three genetic lags $L_i^{(p)}$ as: $L_i^{(p)} = M_i^{(p)} - M_1^{(p)}$ for $i = 2, 3, 4$. The $M^{(p)}$ are the mean genetic levels of the different cohorts numbered from 1 to 4 for objective p. The asymptotic result is:

$$\begin{pmatrix} \Delta G^{(p)} \\ L_2^{(p)} \\ L_3^{(p)} \\ L_4^{(p)} \end{pmatrix} = \begin{pmatrix} u_1 & -\boldsymbol{T}_{12} \\ \boldsymbol{U}_2 & (\boldsymbol{I}_3 - \boldsymbol{T}_{22}) \end{pmatrix}^{-1} \underline{\mathcal{E}}^{(p)} \qquad [13]$$

where

$$\boldsymbol{T} = \begin{pmatrix} t_{11} & \boldsymbol{T}_{12} \\ \boldsymbol{T}_{21} & \boldsymbol{T}_{22} \end{pmatrix} \quad \text{and} \quad \boldsymbol{U} = \begin{pmatrix} u_1 \\ \boldsymbol{U}_2 \end{pmatrix}$$

$\boldsymbol{T}$ is the 'gene flow' transition matrix. Each element t_{ij} represents the average fraction of genotype of progeny i that comes from parents j; thus $t_{ij} = 0.5 w_{ij}$ where the w_{ij} are the probabilities of gene transmission previously defined. $\boldsymbol{T}$ is partitioned into four sub-matrices: t_{11} is a scalar, $\boldsymbol{T}_{12}$ is a row vector with elements t_{1k}, $\boldsymbol{T}_{12}$ is a column vector with elements t_{k1}, and $\boldsymbol{T}_{22}$ is a matrix of size 3×3.

$\boldsymbol{U}$ is the column vector of the generation intervals weighted by the above probabilities of gene transmission; u_1 is the average generation interval for cohort 1, $\boldsymbol{U}_2$ is the vector for the three other cohorts.

$\underline{\mathcal{E}}^{(p)} = \left\{ \mathcal{E}_{ij}^{(p)} \right\}$ is the vector of the corresponding average genetic selection differentials for breeding objective p.

Reduction of genetic variances under selection

Under the usual assumptions of an infinitesimal genetic model and a population of infinite size, genetic parameters are modified as a result of the linkage disequilibrium generated by selection (Bulmer, 1971). Ignorance of this reduction of genetic variance may lead to an overestimation of the expected genetic gain. In order to investigate the magnitude of the so-called 'Bulmer effect' in the breeding plan where selection intensities are relatively high, the initial genetic variances and covariances must be replaced by their asymptotic values, which depend on the selection intensities.

By extension of the Bulmer (1971) approach, the genetic covariance between traits l and k for progeny in cohort i is (Phocas, 1995):

$$\sigma_{kl(i)} = 0.25\ \sigma^{\mathrm{d}}_{kl(i)} + 0.25\ \sigma^{\mathrm{s}}_{kl(i)} + 0.5\ \sigma^{0}_{kl} \qquad [14]$$

$\sigma^{\mathrm{s}}_{kl(i)}$ and $\sigma^{\mathrm{d}}_{kl(i)}$ are the genetic covariances between traits l and k for sires and dams selected to give progeny in cohort i. σ^0_{kl} is the genetic covariance in the base population (prior to selection). 0.5 σ^0_{kl} is the within-family variance, which is assumed to remain unchanged under selection when inbreeding does not accumulate, ie, when population is of infinite size.

Computation of $\sigma_{kl(i)}$ requires the computation of the covariance between traits l and k for selected parents in a given mating at t_2 or t_4, and the appropriate combination of these covariances for all possible parents.

Genetic variances for selected candidates in a given pair

Using the expression of Tallis (1961) for the second moments of a truncated multivariate normal distribution, it is possible to compute $\mathrm{E}(X_l X_k)$ where X_l and X_k are two (assumed normal) variates with known correlation ρ_{kl}, when selection is based on the n predictors I_i, $i = 1, \ldots, n$. Correlations between X_l and the predictors are noted $\rho_{X_l i}$. We have:

$$\begin{aligned}\mathrm{E}(X_k X_l) &= \rho_{kl} \\ &+ \frac{1}{\mathcal{Q}} \sum_{q=1}^{n} \rho_{X_l q}\ \rho_{X_k q}\ c_q\ z_q\ \mathcal{Q}_{n-1,q} \\ &+ \frac{1}{\mathcal{Q}} \sum_{q=1}^{n} \left\{ \rho_{X_k q} \sum_{r \neq q} (\rho_{X_l r} - \rho_{qr}\rho_{X_l q})\ \phi(c_q, c_r; \rho_{qr})\ \Phi_{n-2}(\boldsymbol{\theta}^q_{rs}; \boldsymbol{R}_{qr}) \right\}\end{aligned} \qquad [15]$$

$\boldsymbol{R}_{qr}$ is the matrix of partial correlation coefficients of I_s given I_q and I_r for $s \neq q$ and $s \neq r$. The c values are the truncation thresholds (c_{is}, c'_{is}, and c_{ai_s} $s = ♂, ♀$) derived in equations [1] to [4], [6] and [7]. The z and $\mathcal{Q}_{n-1,j}$ values were defined in [11], and:

$$\boldsymbol{\theta}^q_{rs} = \frac{c_s - \beta_{sq.r} c_q - \beta_{sr.q} c_r}{\sqrt{(1-\rho^2_{sq})(1-\rho^2_{sr.q})}}$$

In the above formula, $\beta_{sq.r}$ and $\beta_{sr.q}$ are the partial regression coefficients of I_s on I_q given I_r and of I_s on I_r given I_q, respectively, and $\rho_{sr.q}$ is the partial correlation coefficient between I_s and I_r given I_q. $\boldsymbol{\theta}^q_{rs}$ is the vector [of size $(n-2)$] of thresholds to be used in the cumulative normal probability function Φ_{n-2}.

Once these expectations are computed, the covariance is given by

$$\mathrm{cov}(X_k, X_l) = \mathrm{E}(X_k X_l) - \mathrm{E}(X_k)\ \mathrm{E}(X_l) \qquad [16]$$

Variance of the sires and dams of a given progeny cohort

The next step is to compute the matrices $\boldsymbol{V}^{\mathrm{s}}_{(i)}$ and $\boldsymbol{V}^{\mathrm{d}}_{(i)}$ of genetic variances for selected sires and dams of a given progeny cohort i, ie, the distribution variances resulting from a mixture of several elementary distributions with known

expectations and variances. Let $\boldsymbol{V}^{\mathrm{d}}_{(i)}(l,k)$ be the covariance matrix between traits l and k among dams of cohort i:

$$\boldsymbol{V}^{\mathrm{d}}_{(i)}(l,k) = \sum_{j=1,2} w_{ji}\left(\boldsymbol{V}^{\star}_{ji}(l,k) + \boldsymbol{E}^{\star}_{ji}(l)\boldsymbol{E}^{\star}_{ji}(k)\right) - \left(\sum_{j=1,2} w_{ji}\boldsymbol{E}^{\star}_{ji}(l)\right)\left(\sum_{j=1,2} w_{ji}\boldsymbol{E}^{\star}_{ji}(k)\right) \quad [17]$$

In the above formula, $\boldsymbol{V}^{\star}_{ji}(l,k)$ is the covariance between traits l and k for females from cohort j selected to give progeny in cohort i, and $\boldsymbol{E}^{\star}_{ji}(l)$ is the mean breeding value for trait l of females from cohort j selected to give progeny in cohort i. $\boldsymbol{E}^{\star}_{ji}(l)$ and $\boldsymbol{V}^{\star}_{ji}(l,k)$ were obtained as shown previously. A similar expression is obtained for $\boldsymbol{V}^{\mathrm{s}}_{(i)}(l,k)$.

A matrix formulation of [14] is

$$\boldsymbol{G}^{\star}_{0(i)} = \frac{1}{2}\boldsymbol{G}_0 + \frac{1}{4}\boldsymbol{V}^{\mathrm{d}}_{(i)} + \frac{1}{4}\boldsymbol{V}^{\mathrm{s}}_{(i)} \quad [18]$$

$\boldsymbol{G}_0$ and $\boldsymbol{G}^{\star}_{0(i)}$ are, respectively, the initial and asymptotic matrices of genetic variances and covariances. As explained in the *Appendix*, $\boldsymbol{G}^{\star}_{0(i)}$ is used to compute the variances of the predictors and the covariances between the predictors and the different H_p for the next round of an iterative algorithm.

Computational strategy

The previous equations lead to a three-step algorithm, as in Phocas (1995).

1) Using the method of Ducrocq and Quaas (1988), the truncation thresholds (equations [1]–[4]), the proportions of parents used [8] and the genetic selection differentials [12] are derived, for a given set of genetic variances and covariances.

2) After determining these parameters, the asymptotic genetic gains and lags are computed in equation [13].

3) The genetic variances and covariances are updated in equation [18], as well as the (co)variances of the predictors.

4) Step 1 to 3 are repeated until convergence is reached.

At convergence, the genetic lag at birth between two successive flocks is the asymptotic genetic gain ΔG for all cohorts.

The first step of this algorithm makes use of the asymptotic results derived in the second and third step. Genetic means of all cohorts are first initialized to zero and they are updated at each iteration. The means of the predictors, which are necessary in step 1, must also be updated: EBVs are supposed to be unbiased so, at each stage j of the selection process, $\mathrm{E}(\hat{\boldsymbol{u}}_j) = \mathrm{E}(\boldsymbol{u}_j)$, where $\boldsymbol{u}_j$ is the genetic merit at step j. The genetic lags for each trait i are required to obtain these desired quantities: if $\bar{\boldsymbol{u}}_{(k)}$ is the vector of genetic means for the seven different traits in cohort k, expressed as a deviation from the reference cohort 1, the mean $\boldsymbol{\mu}_{j(k)}$ of

the predictor used at stage j is then $\boldsymbol{\mu}_{j(k)} = \boldsymbol{b}'\bar{\mathbf{u}}_{(k)}$, where $\boldsymbol{b}$ is the vector of weights used to compute the aggregate genotype.

If step 3 is skipped, ie, if the genetic variances are supposed to be stable under selection, convergence is quickly reached (4 to 6 rounds for a total of 25 CPU min on an IBM RS 6000 are necessary). Otherwise the algorithm takes longer to converge (10 to 12 rounds for a total of 75 CPU min).

NUMERICAL APPLICATIONS

In this section, the influence of several factors on the annual expected genetic gain is investigated. The assumed demographic parameters are given in table I.

Table I. Demographic parameters of the modelled breeding plans.

Initial number of female chicks	$N_{0♀}$	2 200
Initial number of male chicks	$N_{0♂}$	2 200
Number of females measured on laying traits	$N_{♀}$	500, 700, 1 000, 1 500
Number of females mated to each sire	d	3,...,7
Number of pedigree breeding females	N_d	300, 400
Female survival rate at t_1	$S_{1♀}$	0.75
Male survival rate at t_1	$S_{1♂}$	0.71
Female survival rate at t_3	$S_{3♀}$	0.73
Male survival rate at t_3	$S_{3♂}$	0.69
Survival rate of a pair during the first egg collection period	$S_1^\star$	0.96
Survival rate of a pair during the second egg collection period	$S_2^\star$	0.94
Prolificacy of young dams	p_y	6.5
Prolificacy of old dams	p_o	4.6
Initial proportion of males from the first egg collection	$\alpha_{♂}$	$0.2 \leqslant \alpha_{♂} \leqslant 1$
Initial proportion of females from the first egg collection	$\alpha_{♀}$	$0.2 \leqslant \alpha_{♂} \leqslant 1$

Breeding objective

The breeding objective H is of the form $H = \boldsymbol{\kappa}'\mathbf{a}$ where $\boldsymbol{\kappa}$ is the vector of economic weights and $\mathbf{a}$ represents the genetic merit. If ranking of candidates is based on BLUP EBVs, the corresponding index is $I = \boldsymbol{\kappa}'\hat{\mathbf{a}}$.

The genetic parameters for these traits were estimated using a REML procedure on a large data set (Chapuis, 1997) and are given in table II.

Table II. Estimates of heritabilities (on diagonal) and genetic correlations for male and female body weight (BW) at 12 and 16 weeks of age, and Box–Cox transformed egg numbers (EN_1, EN_2 et EN_3).

Traits	BW*12*♀	BW*12*♂	BW*16*♀	BW*16*♂	EN*1*	EN*2*	EN*3*
$BW12_♀$	**0.43**	0.89	0.96	0.90	−0.41	−0.33	−0.21
$BW12_♂$		**0.36**	0.82	0.94	−0.30	−0.15	−0.04
$BW16_♀$			**0.51**	0.90	−0.45	−0.33	−0.21
$BW16_♂$				**0.40**	−0.38	−0.20	−0.10
EN_1					**0.20**	0.69	0.45
EN_2						**0.19**	0.96
EN_3							**0.18**

The approach used here consists in testing several sets of weights in order to observe the predictable evolution of the different traits of interest. Let us assume that the breeding objective is given by:

$$H = \sum_{i=1}^{7} b_i a_i = \sum_{i=1}^{7} b_{i0} a_i / \sigma_{a_i}$$

constraining the sum of the b_{i0} values to be 1.

Let γ be a positive number ($\gamma < 0.25$). The b_{i0} values are arbitrarily chosen as follows: for the four body weights ($BW12_♀$, $BW12_♂$, $BW16_♀$ and $BW16_♂$), $b_{i0} = \gamma$, for EN_1 and EN_2, $b_{i0} = 0.25\ (1 - 4\gamma)$, and for EN_3 $b_{i0} = 0.5\ (1 - 4\gamma)$ because EN_3 corresponds to a period twice as long as EN_1 or EN_2.

If $\gamma = 0$, the breeding objective is completely focused on laying traits. If $\gamma = 0.25$, the breeding objective includes only body weights.

The corresponding expected genetic gains for each trait are displayed in figure 4 for different γs and given αs. When γ increases, the expected genetic gain in EN_1 decreases more quickly than those in EN_2 and EN_3, certainly because these latter traits are less negatively correlated with body weight. When $0.06 < \gamma < 0.11$, both growth and laying traits are improved, and for $\gamma = 0.25$, the expected genetic gain is about 1.7 genetic standard deviation (σ_G) for the different body weight traits and, respectively, $-0.72\sigma_G$, $-0.46\sigma_G$ and $-0.26\sigma_G$ for EN_1, EN_2 and EN_3.

Reduction of genetic variances under selection

Two points were studied: the asymptotic heritabilities and correlations of selected traits and the estimated genetic gain accounting for the reduction of the genetic variances. The reduction of genetic variances in cohort 4 (the most intensively selected cohort) for the different γs is shown in figure 5.

For growth traits, the reduction of genetic variances is about 6% when $\gamma = 0$, and 25% when $\gamma = 0.25$. It is minimal when $\gamma = 0.05$. At this point, the asymptotic genetic variances are close to their initial values. This is also a situation where ΔG is near zero for growth traits.

For laying traits, the maximum reduction ranges from 10 (for EN_1) to 15% (for EN_3) when $\gamma = 0$. A minimal decrease is observed when γ is about 0.15. As

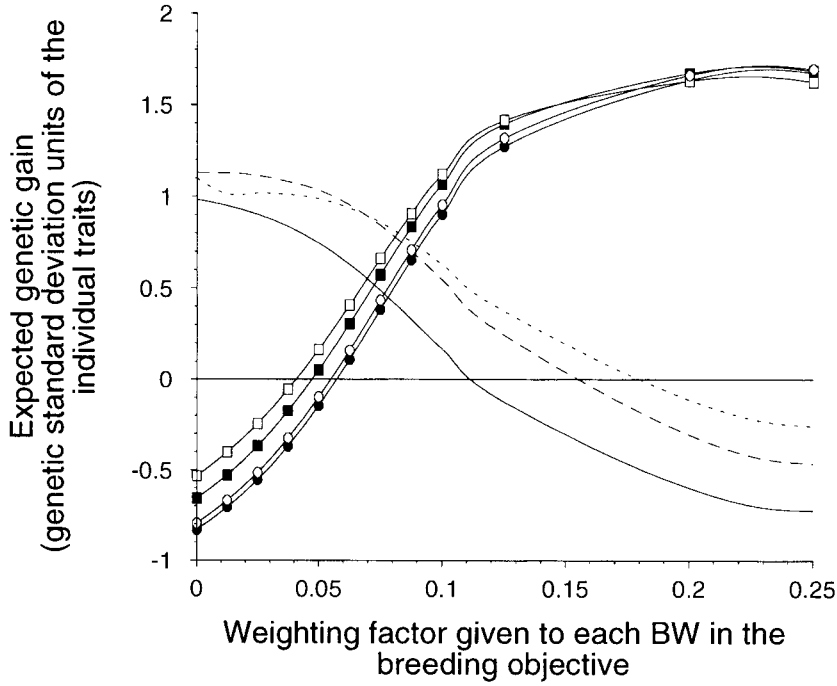

Fig 4. Expected genetic gain for each trait (in genetic standard deviations): male and female body weight (BW) measured at 12 and 16 weeks, and three partial egg numbers, EN_1, EN_2 and EN_3. γ is the standardized weight given to each body weight in the breeding objective. Genetic parameters are given in table II and are assumed to remain stable under selection. $N_{♀} = 1\,000$; $N_d = 300$; $\alpha_{♀} = \alpha_{♂} = 0.6$; $d = 5$. —○—, $BW12_{♀}$; —□—, $BW12_{♂}$; —●—, $BW16_{♀}$; —■—, $BW16_{♂}$; —, EN_1; – –, EN_2; - - -, EN_3.

for laying traits, this minimal decrease close to zero corresponds to a null genetic gain for these traits. The magnitude of the reduction is 2–7% when $\gamma = 0.25$. The corresponding expected genetic gains are given in table III.

The expected genetic gains with varying γ and reduction of genetic variances under selection are displayed in figure 6.

The asymptotic genetic correlations are given in table IV for $\gamma = 0$, $\gamma = 0.075$ and $\gamma = 0.25$. It can be seen that when selection is entirely focused on laying traits, changes in genetic parameters due to selection are noticeable. In contrast, these changes are less important when $\gamma = 0.075$ (ie, when selection is more balanced) even if the asymptotic genetic correlations between growth traits and laying traits are slightly more negative than the initial parameters reported in table II.

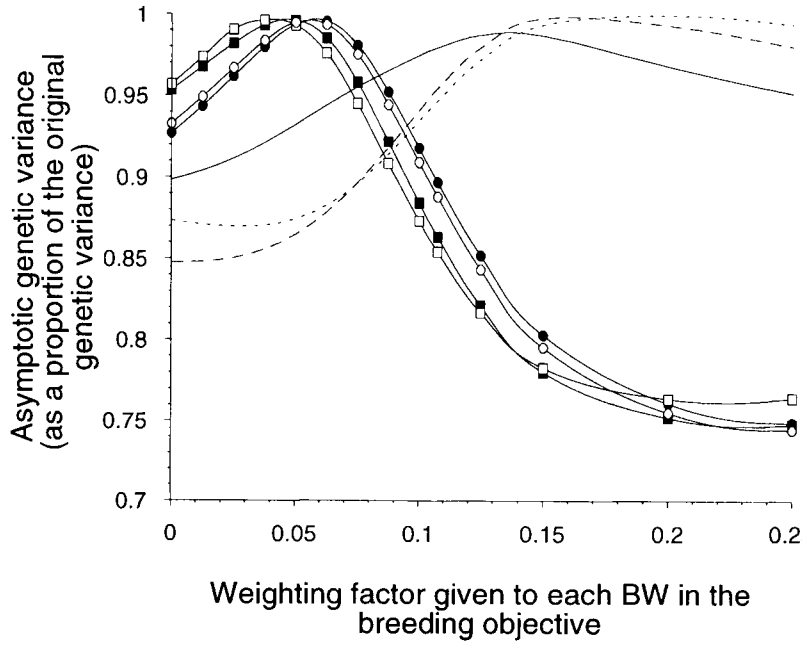

Fig 5. Reduction of genetic variances under selection for each trait: male and female body weight (BW) measured at 12 and 16 weeks, and three partial egg numbers, EN_1, EN_2 and EN_3. γ is the standardized weight given to each body weight in the breeding objective. $N_{♀} = 1\,000$; $N_d = 300$; $\alpha_{♀} = \alpha_{♂} = 0.6$; $d = 5$. —o—, $BW12_{♀}$; —□—, $BW12_{♂}$; —•—, $BW16_{♀}$; —■—, $BW16_{♂}$; —, EN_1; – –, EN_2; - - -, EN_3.

Demographic parameters

Proportion of different candidate cohorts at birth

Until now, $\alpha_{♂}$ and $\alpha_{♀}$ were assumed to be fixed and known. They determine the selection intensities imposed on sires and dams selected during the first and the second reproduction periods. In addition, the possible range for α_s ($s = ♂, ♀$) is determined by the number of chicks initially reared ($N_{0♂}$ and $N_{0♀}$) and the number N_d of pedigree breeding females:

$$\frac{\alpha_s N_{0s}}{N_d S_1^{\star} p_y} \leqslant 1 \Rightarrow \max(\alpha_s) = \frac{N_d S_1^{\star} p_y}{N_{0s}} \qquad [19]$$

and

$$\frac{(1-\alpha_s) N_{0s}}{N_d S_2^{\star} p_o} \leqslant 1 \Rightarrow \min(\alpha_s) = 1 - \frac{N_d S_2^{\star} p_o}{N_{0s}} \qquad [20]$$

For $N_d = 400$, the αs range from 0.2 to 1; for $N_d = 300$ the range is only from 0.4 to 0.85.

Table III. Impact of the Bulmer effect on the expected genetic gain (in genetic standard deviation) and the genetic variances for male and female body weight (BW) at 12 and 16 weeks of age, and Box–Cox transformed egg numbers (EN_1, EN_2 and EN_3).

		BW*12*♀	BW*12*♂	BW*16*♀	BW*16*♂	EN*1*	EN*2*	EN*3*
	$\Delta G_{(\infty)}$	−0.66	−0.44	−0.70	−0.55	0.72	0.84	0.73
$\gamma = 0$	$\Delta G_{(0)}$	−0.80	−0.53	−0.83	−0.66	0.98	1.13	1.10
	$\sigma^2_{G_\infty}/\sigma^2_{G_0}$	0.93	0.96	0.93	0.95	0.90	0.85	0.87
	$\Delta G_{(\infty)}$	0.37	0.56	0.32	0.48	0.29	0.57	0.60
$\gamma = 0.075$	$\Delta G_{(0)}$	0.43	0.66	0.38	0.57	0.49	0.84	0.86
	$\sigma^2_{G_\infty}/\sigma^2_{G_0}$	0.97	0.94	0.98	0.96	0.95	0.90	0.90
	$\Delta G_{(\infty)}$	1.45	1.38	1.43	1.44	−0.55	−0.35	−0.19
$\gamma = 0.25$	$\Delta G_{(0)}$	1.69	1.62	1.67	1.68	−0.73	−0.46	−0.26
	$\sigma^2_{G_\infty}/\sigma^2_{G_0}$	0.74	0.76	0.75	0.75	0.95	0.98	0.99

$\Delta G_{(\infty)}$ = asymptotic genetic gain accounting for the Bulmer effect. $\Delta G_{(0)}$ = asymptotic genetic gain when genetic variances are assumed to remain stable under selection. γ determines the weights of the different traits in the breeding objective. When $\gamma = 0$, only laying traits are included in the breeding objective; if $\gamma = 0.25$, the selection is only focused on body weights.

When $\gamma = 0.075$ and $N_d = 400$ (cf fig 7), the highest values for the genetic gain on the aggregate genotype are obtained when both $\alpha_♀$ and $\alpha_♂$ are between 0.5 and 0.6. The lowest value is obtained when $\alpha_s = \max(\alpha_s)$. This corresponds to a decrease of 6.5% of the expected gain.

A similar curve is obtained with $N_d = 300$. The curve displayed in figure 7 accounts for the reduction of genetic variances under selection. The shape of the curve is the same if genetic variances are assumed stable. If we look at each trait separately, no noticeable variation is detected for body weights, and a slight decrease is observed for laying traits EN_1 and EN_2 when the αs reach their maximum.

Therefore it can be considered that the knowledge of optimal αs is not essential, as a value of $\alpha_s = 0.5$ or $\alpha_s = 0.6$ ensures a genetic gain close to the maximum.

Number of dams mated to each sire

In the previous applications, each male was assumed to be mated with five females ($d = 5$). In a female turkey strain this parameter, which determines the selection intensity on the sires, does not exceed seven. In figure 8, the expected genetic gain for the aggregate genotype increases when the number of dams mated to each sire varies from three to seven. The range of the variation is 6%.

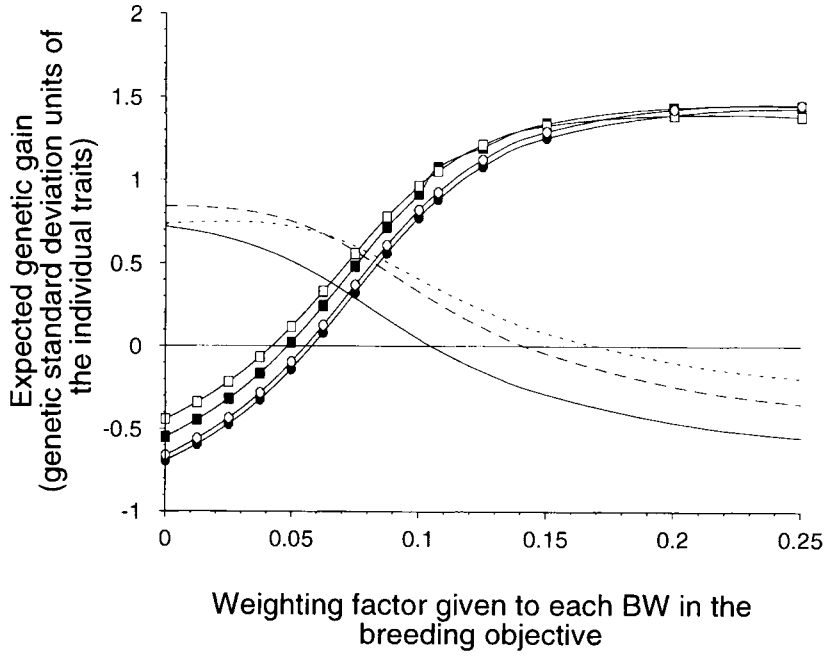

Fig 6. Expected genetic gain for each trait (in genetic standard deviations): male and female body weight (BW) measured at 12 and 16 weeks, and three partial egg numbers, EN_1, EN_2, and EN_3. γ is the standardized weight given to each body weight in the breeding objective. Genetic parameters are assumed to vary under selection. $N_♀ = 1\,000$; $N_d = 300$; $\alpha_♀ = \alpha_♂ = 0.6$; $d = 5$. —○—, $BW12_♀$; —□—, $BW12_♂$; —●—, $BW16_♀$; —■—, $BW16_♂$; —, EN_1; – –, EN_2; - - -, EN_3.

Number of females measured for laying traits

The number of females measured for laying traits deserves attention, as this parameter is likely to influence the overall efficiency of the breeding plan. When this parameter is increased, evaluation of genetic merit for laying traits accounts for a greater number of candidate performances. This increases the correlation between the predictors of genetic merit and the breeding objective, especially if a large emphasis is placed on laying traits in the objective. The genetic (and economic) gain obtained when a larger number of females are selected at t_1 is, however, balanced with the extra costs of maintaining more candidates alive. Economic data being unavailable, it is not the intention of this paper to discuss the relevance of increasing $N_♀$. Nevertheless, it can be shown (cf table V) that this parameter does have an influence on the expected results: when $N_♀$ increases from 500 to 1 500, one can expect an extra gain of 17% for the number of eggs laid, which is balanced with a smaller genetic gain in BW (−12% for $BW16_♂$ and −17% for $BW12_♀$). This shows that $N_♀$ must be accounted for when deriving the relevant weights b_{i0} for a constrained ΔG (eg, with no trend for EN_i).

Table IV. Asymptotic genetic parameters for the traits under selection (male and female body weight (BW), measured at 12 and 16 wk, and three partial egg numbers, EN_1, EN_2 and EN_3), after reduction of genetic variances (Bulmer effect).

Traits	$BW12_f$	$BW12_m$	$BW16_f$	$BW16_m$	EN_1	EN_2	EN_3
	0.42	0.89	0.96	0.90	−0.37	−0.27	−0.15
		0.36	0.82	0.94	−0.27	−0.11	0.01
			0.49	0.89	−0.41	−0.27	−0.15
$\gamma = 0$				**0.39**	−0.36	−0.14	−0.03
					0.18	0.64	0.38
						0.16	0.95
							0.16
	0.43	0.89	0.96	0.90	−0.43	−0.38	−0.26
		0.35	0.82	0.94	−0.33	−0.21	−0.10
			0.5	0.89	−0.47	−0.37	−0.25
$\gamma = 0.075$				**0.39**	−0.42	−0.25	−0.14
					0.19	0.67	0.42
						0.16	0.95
							0.17
	0.36	0.85	0.95	0.87	−0.35	−0.30	−0.21
		0.30	0.77	0.92	−0.23	−0.10	−0.01
			0.44	0.85	−0.40	−0.30	−0.20
$\gamma = 0.25$				**0.34**	−0.33	−0.15	−0.06
					0.19	0.68	0.44
						0.18	0.96
							0.18

γ is the standardized marginal weighting given to each body weight in the breeding objective.

Alternative breeding schemes

The possible advantages of two alternative breeding plans were studied: the first option is to use only young sires, and the second is to perform selection on laying performances before matings instead of the proposed mate selection.

Use of 'young' sires only

We considered the possibility of using sires from flock F_{n+1} only to create F_{n+4}. Layers remain either 'young' or 'old', but old dams of flock F_n are mated with males from flock F_{n+1} selected on their EBVs at t_1. This option aims at reducing the generation interval. This gain is balanced with the loss of accuracy on the selection of the males, and with the loss of selection intensity, as males selected at t_1 must produce enough semen to inseminate $2 \times N_d$ females (N_d contemporary young females and N_d females from the preceding flock). It is thus necessary to increase the number of males selected at t_1.

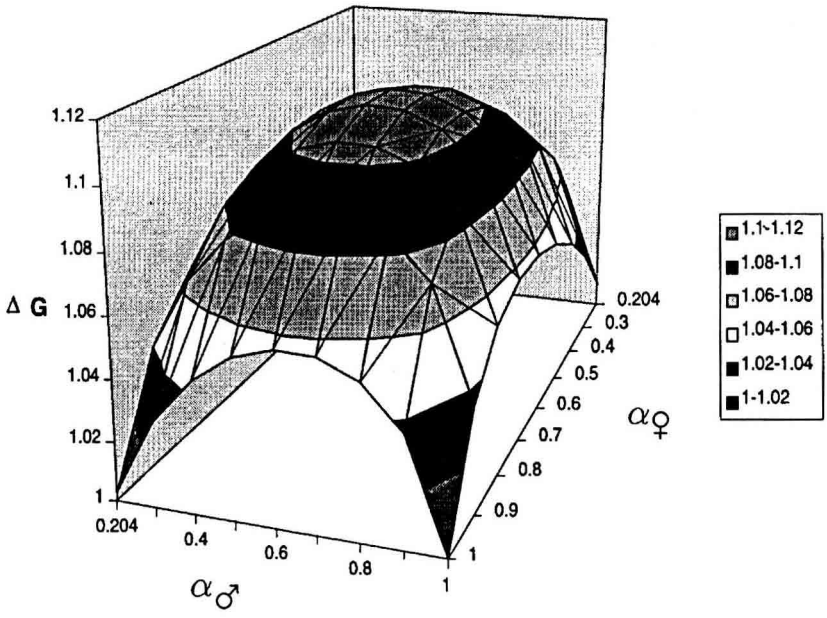

Fig 7. Expected genetic gain for aggregate genotype (in genetic standard deviations). $N_{♀} = 1\,000$; $N_d = 400$; $\gamma = 0.075$, $d = 5$.

It can be seen, in figure 9, that this breeding plan (breeding plan 2) offers no advantage compared to the one defined previously (breeding plan 1). Genetic gains on both growth traits and laying traits are larger with breeding plan 1.

No mate selection

In this part, we intend to evaluate the advantage of the selection of best mated pairs. The initial breeding plan is thus compared to a scheme where only individual selection is performed (breeding plan 3) and to a scheme where the 1 000 females measured on laying traits are inseminated with identified semen (breeding plan 4). In breeding plan 4, all the females measured for laying traits are candidates for mate selection, which is more intense than in breeding plan 1 where only 300 females are candidates.

It can be seen in figure 9 that the expected genetic gain for the overall breeding objective H_1 obtained with breeding plan 1 is 6% larger than that obtained with breeding plan 3. The genetic gain on H_1 obtained with breeding plan 4 is only 2% higher than that obtained with breeding plan 1. If one looks closely at each trait separately, the picture is different. Genetic gains are larger for laying traits with breeding plan 4, and lower for growth traits. In breeding plan 4, the selection intensity is applied mainly at t_2 and t_4, while the greatest selection intensity is performed at t_1 in the breeding plan 1. At t_1, only growth traits are measured, and

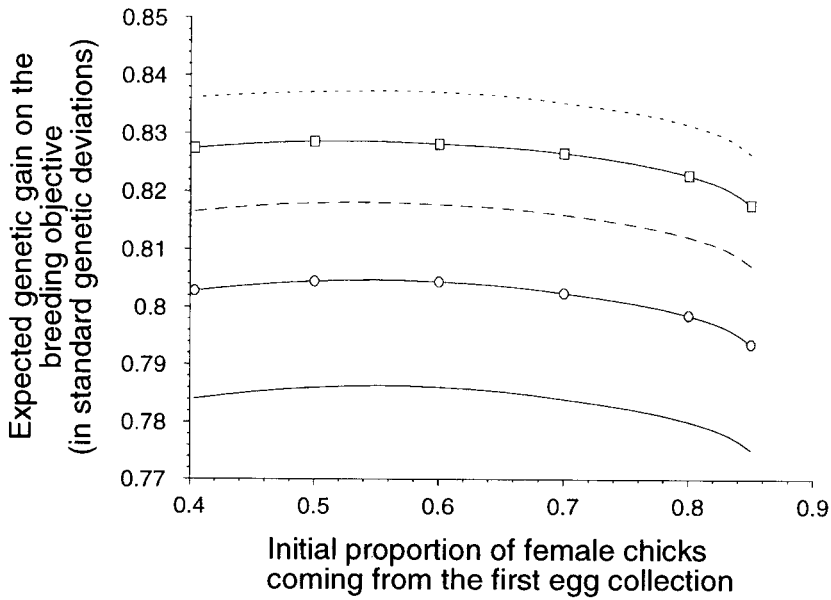

Fig 8. Expected genetic gain for aggregate genotype when the number d of dams mated to each sire varies from 3 to 7. $N_{♀} = 1\,000$; $N_d = 300$; $\alpha_{♂} = 0.6$; $\gamma = 0.075$.
—, $d = 3$; —o—, $d = 4$; – –, $d = 5$; —□—, $d = 6$; - - -, $d = 7$.

Table V. Expected annual genetic gain on the traits of interest (male and female body weight (BW) at 12 and 16 weeks of age, and $\sum(EN)$, which is the total egg number on the original scale), when $N_{♀}$, the number of females measured on laying traits varies.

$N_{♀}$	BW$12_{♀}$ *(g)*	BW$12_{♂}$ *(g)*	BW$16_{♀}$ *(g)*	BW$16_{♂}$ *(g)*	$\sum$(EN)*(eggs)*
500	114	283	118	318	2.04
700	108	271	112	305	2.15
1000	102	260	106	292	2.29
1500	96	249	100	280	2.39

$N_d = 300$; $\gamma = 0.075$.

thus the predictor I_{1s} of aggregate genotype is not as correlated with laying traits as it is in later stages. A higher gain for laying traits is then expected when a more intense selection is applied after t_1. In such circumstances, it might be possible to improve laying traits even while giving relatively less emphasis to these traits.

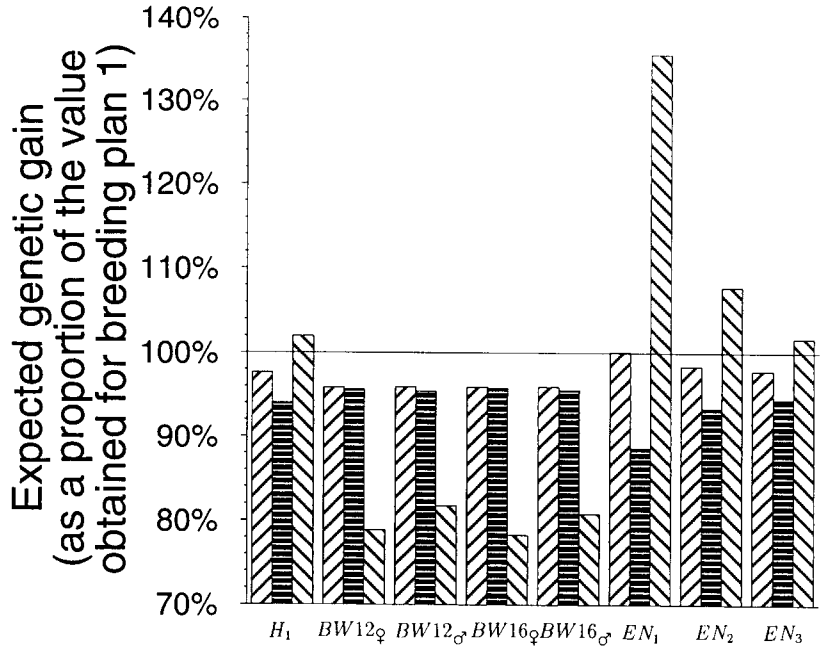

Fig 9. Comparison of breeding plan 1 where old sires are being used, with breeding plan 2, where only young sires are used, breeding plan 3 where no selection of mated pairs is performed, and with breeding plan 4 where selection of mated pairs is performed for all females. $N_♀ = 1\,000$; $N_d = 300$ in breeding plans 1, 2 and 3 and $N_d = 1\,000$ for breeding plan 4; $\gamma = 0.075$; $\alpha_♂ = \alpha_♀ = 0.6$; H1 = breeding objective. The traits considered are male and female body weight (BW) measured at 12 and 16 weeks, and three partial egg numbers (EN).
▨, Breeding plan 2; ▬, breeding plan 3; ▧, breeding plan 4.

DISCUSSION

This study aimed to predict genetic gain and lags in a meat-type poultry breeding scheme where selection was based on BLUP estimates with overlapping generations. This involved several simplifying assumptions that will be reviewed here.

Inbreeding rate and variability of family size

In the computations above, neither the rate of inbreeding nor the variability of family size were accounted for. These two points are linked and are both likely to influence ΔG.

If no assortative matings are performed, and if d is not too large, considering that each selected male belongs to an equal number of successful pairs may be a

reasonable assumption. Nevertheless, one understands that a male exhibiting a very high EBV will be successful, whatever females it is mated with. For this male, the number of successful pairs is d and not $\mathrm{E}(d) = d^{\star}$. If no restriction is made on the number of selected offspring of such a male, an increase in ΔG is expected in the short term, and also a predictable increase in ΔF, which should be avoided as it leads, in the long term, to a deterioration of viability and reproductive ability.

In our study, where generations overlap, evaluation is made upon multiple trait BLUP EBVs, and the real number $N_{♂}$ of males selected is not precisely known. An exact derivation of the inbreeding rate through deterministic calculations is very complex. It is not the intention of this paper to establish such a formula, although its need is acknowledged.

It was seen that increasing the number of females mated to each male from three to seven, and therefore selecting fewer males, led to an increase of 6% in the expected genetic gain. This gain is unfortunately balanced with a predictable increase in the inbreeding rate. Therefore, it seems preferable not to reduce the number of male parents by inflating the number of females mated to each sire. Along the same lines, the use of 'young' sires only was shown to result in a lower genetic gain than the initial breeding plan, where both 'young' and 'old' sires are used. In addition, this is unfortunately likely to increase inbreeding, as all sires come from the same flock. In the present case, it is therefore not relevant to reduce the generation interval in the way described in the alternative breeding plan.

Another way to attack the problem is to use Monte-Carlo stochastic simulations to predict genetic gain and lags of a given breeding plan. These methods are more flexible and allow for the computation of an inbreeding coefficient. The variability of family size can be accounted for. They are, however, more time consuming as they require a large number of replicates to ensure the reliability of the results and to achieve optimization of the selection with regard to the truncation thresholds.

Effects of selection on the genetic variance

Selection affects the genetic variance directly by changing gene frequencies and inducing a linkage disequilibrium between the selected loci (Lush, 1945; Bulmer, 1971). Selection also acts indirectly on the variance by changing the family structure and therefore increasing the loss of variation through inbreeding if the population is of limited size (Lush, 1946; Robertson, 1961). It is worth noting that in an evaluation based on mixed model methodology applied to an animal model, these phenomena are magnified (Verrier, 1989). Since all genetic relationships are accounted for, related candidates are likely to be culled or selected together, leading to higher inbreeding rate and loss of genetic variance, which limit the long-term gain (Verrier et al, 1993). This emphasizes the need to account for the Bulmer effect in the prediction of ΔG.

Different algorithms exist for predicting the evolution of the additive genetic variance due to selection under the infinitesimal model. Some are discussed by Verrier (1989). The effect of selection on genetic parameters was also investigated by several authors. Villanueva and Kennedy (1990) showed that the asymptotic genetic variances of traits under (direct or indirect) selection is less than these in the base population, and evaluated the change in heritabilities and genetic correlations with

regards to their initial values. One might be surprised, when looking at figure 5, to notice that, for some weightings of the traits in the breeding objective (ie, for some values of γ), no reduction of variance is observed. Such a situation can be explained if the correlation between the predictor and the considered trait is constrained to zero. It can be seen in figure 6 that the γs inducing no reduction of genetic variance for the different traits also correspond to a null genetic gain for these traits. When $\gamma = 0$ or $\gamma = 0.25$, the situation is the one described by Villanueva and Kennedy (1990) and our results are in good agreement with theirs.

The impact of selection on the genetic correlation between body weight and laying ability could be experimentally assessed by divergent selection for body weight (BW) or egg number (EN). According to Nestor et al (1996), who selected for many generations one turkey strain for 180 days EN and another for 16 weeks BW, the correlation between BW and EN varied considerably from null to strongly negative and fluctuated between these two extremes. A strong negative genetic correlation between EN and BW, resulting from a long and intense selection carried out on BW, was also observed by Chapuis et al (1996).

The impact of selection on genetic variances was shown to be different among the traits considered. Therefore, not accounting for the Bulmer effect has two major deleterious effects on the reliability of the prediction: 1) an overestimation of the genetic gain and 2) the use of an incorrect set of genetic parameters, which prejudices the correct elaboration of the breeding objective.

Selection of mated pairs

Under selection of mated pairs, hatched chicks are selected using the best available estimates of their breeding value. The pedigree information used to compute the BLUP estimates is common to all offspring of a given mate. Thus, all progeny of a given pair are either selected or eliminated. This is likely to increase ΔF. Nevertheless, it is possible to change the mating pairs between the two reproductive periods. Second matings can be either random or preferential, using the information available at t_3. In the latter case, the assumption of an equal number of successful matings for each sire is even more likely to be invalid.

Toro and Perez-Enciso (1990) suggest planning the matings using linear programming. They maximize the sum $\hat{u}_s + \hat{u}_d$ under the constraint of minimum kinship between the selected sires and dams where $\hat{u}_s$ and $\hat{u}_d$ are the EBVs of the selected sires and dams. This technique is appealing but involves heavy computational costs, which limit its use to small populations. In poultry breeding, however, these constraints may be alleviated because of the particular data structure, where only a restricted fraction of the candidates is selected to sire the next generation. One may introduce a constraint on the kinship between the selected candidates at t_1 in order to select no more than a certain number of full sibs. Breeders have their own empirical rules, the relevance of which will not be discussed here. More generally, special attention should be paid to the idea of introducing a constraint on the kinship between the selected sires and dams to design the mating pattern.

CONCLUSION

In this paper a deterministic description of a poultry selection scheme is given. The resulting algorithm is rather complex, as it aims to account for some important features of the scheme considered: 1) the breeding plan is sequential; 2) it includes correlated traits, some of them being negatively correlated (eg, growth and reproduction traits); 3) the genetic evaluation of candidates is based on a multiple trait BLUP procedure; 4) generations overlap; 5) the Bulmer effect is accounted for.

Several breeding plans were compared. Results showed that the initial proportions of candidate cohorts did not have a large impact on expected genetic gains. This allowed a within-flock selection of candidates. Should the initial proportions of candidate cohorts ($\alpha_{♂}$ and $\alpha_{♀}$) have a predominant influence on the expected genetic gain, it then would be necessary to compare the chicks from two successive flocks. A within-flock selection is much simpler to implement and, in this study, only slightly sub-optimal if $\alpha_{♂} = \alpha_{♀} = 0.6$.

We also proposed a selection procedure (selection of best mated pairs) to select hatched eggs, based on the mean additive genetic merit of their parents. Selection of mated pairs was shown to increase the expected genetic gain for laying traits. When the objective of the selection is to improve laying ability, it is more relevant to increase the amount of information on laying performances, by increasing the number of females measured for egg traits, and to apply selection of mated pairs, rather than reducing generation intervals.

This deterministic modelling can be viewed as an essential screening tool, and more precise analyses could be performed through stochastic modelling, in order to overcome some of the limitations encountered (eg, evolution of the inbreeding rate ΔF, and its effect on ΔG). Stochastic simulations could also provide a useful check of the results of the rather complex algorithm used here.

More generally, the numerical applications present the different genetic trends that can be expected for each trait in various situations. This allows breeders to precisely assess and foresee the consequences of any change in their breeding plan for the annual genetic gain.

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APPENDIX: Derivation of the variances of predictors

The (co)variance matrix of the predictors used at each stage of the sequential selection scheme is required. At each stage j, candidates are ranked based on I_j which combines the estimated breeding values for each trait. $I_j = \boldsymbol{b}_j'\hat{\mathbf{a}}_j$, where $\boldsymbol{b}_j$ is the vector of coefficients used at stage j and $\hat{\mathbf{a}}_j$ the estimated breeding value at stage j. We want to compute:

$$\mathrm{cov}(I_j, I_k) = \boldsymbol{b}_j'\mathrm{cov}(\hat{\mathbf{a}}_j, \hat{\mathbf{a}}_k')\boldsymbol{b}_k$$

and

$$\mathrm{cov}(H, I_j) = \boldsymbol{\kappa}'\mathrm{cov}(\mathbf{a}, \hat{\mathbf{a}}_j')\boldsymbol{b}_j$$

where H is the breeding objective, $\boldsymbol{a}$ the vector of true breeding values, and $\boldsymbol{\kappa}$ the vector of economic weights. Andersen (1994) noted that a well-known limitation of deterministic breeding plan modelling is that, in general, no attention is paid to the influence of estimation of fixed effects. As poultry breeding is characterized by large populations subject to few environmental effects (often accounted for in evaluations as unique contemporary groups, ie, hatch effect) the fixed effect may reasonably be assumed to be correctly estimated by the mean of performances of each hatch. Also, as shown by Andersen (1994), we have in such a situation:

$$\mathrm{cov}(\hat{\mathbf{a}}_j, \hat{\mathbf{a}}_k') = \mathrm{var}(\hat{\mathbf{a}}_j) \text{ if } k > j$$

Thus the calculation is tantamount to the computation of the variance of the estimated breeding values at each stage. For that purpose, the prediction error variance (PEV) of the evaluation is needed. If sufficient ancestral information is available, the PEV is stable under selection (Henderson, 1982). According to Dekkers (1992), this greatly simplifies the modelling of AM-BLUP evaluation: it is sufficient to compute the PEV matrix at the beginning of the selection, in an unselected population where information sufficiently cumulates. In order to mimic a multiple trait BLUP evaluation accounting for all information and pedigree, a fictitious pedigree, including several generations of ancestors, is created. In our applications, three generations of ancestors were assumed to be known. Under such conditions, the PEV was not sensitive to extra ancestral information. The PEV matrix is simply obtained by inverting $\boldsymbol{C}$, the coefficient matrix of the mixed model equations.

If $\mathbf{PEV}_j$ represents the block of $\boldsymbol{C}^{-1}$ pertaining to the candidate for which we wish to obtain the (co)variance matrix of predictors at stage j, we have (Henderson, 1975)

$$(\mathrm{var}(\hat{\mathbf{a}}))_j = \boldsymbol{G}_0 - \mathbf{PEV}_j = \mathrm{cov}(\hat{\mathbf{a}}_j, \boldsymbol{a}_j)$$

Thus [A1]

$$\mathrm{var}(I_j) = \boldsymbol{b}_j'(\boldsymbol{G}_0 - \mathbf{PEV}_j)\boldsymbol{b}_j$$

and, for $k > j$

$$\begin{aligned}\mathrm{cov}(I_j, I_k) &= \boldsymbol{b}_j' \mathrm{cov}(\hat{\mathbf{a}}_j, \hat{\mathbf{a}}_k') \boldsymbol{b}_k \\ &= \boldsymbol{b}_j' (\boldsymbol{G}_0 - \mathbf{PEV}_j) \boldsymbol{b}_k\end{aligned} \qquad [A2]$$

The covariance between the breeding objective H and the selection index is then:

$$\begin{aligned}\mathrm{cov}(H, I_j) &= \boldsymbol{\kappa}' \mathrm{cov}(\mathbf{a}, \hat{\mathbf{a}}_j) \boldsymbol{b}_j \\ &= \boldsymbol{\kappa}' (\boldsymbol{G}_0 - \mathbf{PEV}_j) \boldsymbol{b}_j\end{aligned} \qquad [A3]$$

$\mathrm{var}(I_j)$ and $\mathrm{cov}(I_j, I_k)$ are needed to derive the truncation thresholds. $\mathrm{cov}(H, I_j)$ is used to derive the genetic selection differentials.

When the reduction of genetic variances under selection is accounted for, an iterative algorithm is used. If animal breeding evaluation takes into account all information and pedigree from the beginning of selection (as assumed in a BLUP procedure), PEV is calculated before selection and is constant. Therefore, at each round of the iterative algorithm, in equations [A1]–[A3], **PEV** is held constant, and $\boldsymbol{G}_0$ is replaced by its current value $\boldsymbol{G}_{0(i)}^{\star}$ (see *Materials and methods*).