Evaluation of inbreeding in laying hens by applying optimum genetic contribution and gene flow theory

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ABSTRACT Due to consistent increases of inbreeding of on average 0.95% per generation in layer populations, selection tools should consider both genetic gain and genetic relationships in the long term. The optimum genetic contribution theory using official estimated breeding values for egg production was applied for 3 different lines of a layer breeding program to find the optimal allocations of hens and sires. Constraints in different scenarios encompassed restrictions related to additive genetic relationships, the increase of inbreeding, the number of selected sires and hens, and the number of selected offspring per mating. All these constraints enabled higher genetic gain up to 10.9% at the same level of additive genetic relationships or in lower relationships at the same gain when compared with conventional selection schemes ignoring relationships. Increases of inbreeding and genetic gain were associated with the number of selected sires. For the lowest level of the allowed average relationship at 10%, the optimal number of sires was 70 and the estimated breeding value for egg production of the selected group was 127.9. At the highest relationship constraint (16%), the optimal number of sires decreased to 15, and the average genetic value increased to 139.7. Contributions from selected sires and hens were used to develop specific mating plans to minimize inbreeding in the following generation by applying a simulated annealing algorithm. The additional reduction of average additive genetic relationships for matings was up to 44.9%. An innovative deterministic approach to estimate kinship coefficients between and within defined selection groups based on gene flow theory was applied to compare increases of inbreeding from random matings with layer populations undergoing selection. Large differences in rates of inbreeding were found, and they underline the necessity to establish selection tools controlling long-term relationships. Furthermore, it was suggested to use optimum genetic contribution theory for conservation schemes or, for example, the experimental line in our study.

Key words: laying hen, inbreeding, genetic gain, optimal genetic contribution, gene flow

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INTRODUCTION

Muir et al. (2008) evaluated global production of chickens in the past 50 yr, and they found an increase of productivity of 436% since 1970. The main component, accounting for 90% of increased productivity, was intensive selection. For an industry to be successful in the future, Muir et al. (2008) pointed out the importance of sufficient genetic diversity within companies or within commercial chicken lines for meat as well as for egg production. An intensive selection scheme within lines, followed by an extension of superior genes of broilers and layers via a pyramid breeding scheme, increases the risk of loss of genetic diversity through an increase of inbreeding and relationships. If the parents are related, some of the alleles transmitted to the offspring by each parent will be copies of the same alleles found in the common ancestors. As the genetic relationship between parents increases, the likelihood that pairs of alleles in offspring are copies of a single allele in a common ancestor generations back increases. Such alleles are said to be identical by descent and the overall negative effects were summarized by Falconer (1989): loss in genetic variability, higher chance of appearance of detrimental recessive genes in the homozygous state, and inbreeding depression.

The upward trend of the inbreeding level in different layer populations in the range from 0.13 to 1.5% per generation has been carefully evaluated in several studies (Gowe et al., 1993; Nordskorg and Cheng, 1998; Savas et al., 1999; Sewalem et al., 1999; Schmidt and

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Figueiredo, 2005). Results on the effects of inbreeding on the birds' performance in terms of production and reproduction have been estimated by Sewalem et al. (1999) by including the inbreeding coefficient of the hen, the embryo, and the mate as a partial linear regression in the statistical model. The authors reported that significant inbreeding depression due to the hen, the embryo, and the mate was reported within an egg weight selected line for the percentage of fertile eggs, the percentage hatched of fertile eggs set, and the percentage hatched of total eggs set. Results for inbreeding depression were negligible for egg production traits (e.g., egg number, egg weight, or egg mass), but in all investigated lines, an increase of inbreeding was associated with a delay in sexual maturity. Slight inbreeding depressions have also been reported for the traits BW, average egg weight, age at first egg, and the percentage of fertilized eggs in the study by Szwaczkowski et al. (2004) when applying quadratic partial regression analyses. Ameli et al. (1991) investigated cumulative inbreeding in commercial White Leghorn lines under long-term reciprocal recurrent selection. After 23 generations with the avoidance of full- and half-sib matings, the inbreeding coefficient increased on average 0.7% per year. The increase of inbreeding was associated with a reduced egg production of 3 eggs per year. Inbreeding depressions per 10% increase of inbreeding were also analyzed by Savas et al. (1999) for different Leghorn lines and traits related to egg mass, egg weight, and egg count. Values for inbreeding depressions were lower than values for the increase of genetic gain per year and therefore in most cases were not significantly different from zero. Savas et al. (1999) found differences in heritabilities and in the rates of inbreeding coefficients and inbreeding depression when comparing the male line to the female line. For the female line, the only trait showing a significant inbreeding depression was egg count during wk 20 to 24. One possible explanation was the lower frequency of highly inbred birds in the female line.

Results for inbreeding depression are not so unsettling at the moment but could be of increasing impact in the long-term regarding the breeding structure, intensive selection schemes, and the loss of alleles, as described by Muir et al. (2008). In the case of a detrimental level of homozygosity within a breeding program, a simple loophole would be to import genetics from relatively unrelated breeding stocks. However, due to the worldwide concentration in layer and broiler breeding with only few independent breeding companies, the number and availability of independent lines with an appropriate genetic level is highly limited. Therefore, maintenance of sufficient genetic diversity should be a major objective in any commercial poultry breeding scheme.

Similarly to other species characterized by intensive selection (e.g., dairy cattle and swine), all available tools should be used to maximize selection response by considering inbreeding and genetic relationships in the long term. Inbreeding-controlling strategies focused on such ideas as penalizing best linear unbiased prediction (**BLUP**) estimated breeding values for the level of additive genetic relationships between preselected individuals and the population (Meuwissen and Goddard, 1997), restricting the number of selected full- and half-sibs, or reducing the weighting factors for information coming from relatives in genetic evaluations (Brisbane and Gibson, 1995). Caballero et al. (1996) compared several mating systems with respect to the status of inbreeding and selection response. The best method to reduce inbreeding was the minimum coancestry mating strategy and the avoidance of sib matings. However, the most suitable approach for long-term selection strategies is the optimum genetic contribution (**OGC**) methodology, which has been evaluated for dairy cattle breeding programs (König and Simianer, 2006), the Hanoverian horse breeding program for show jumpers (Niemann et al., 2009), and for pig breeding programs with overlapping generations (Simianer et al., 2003). Optimum genetic contribution maximizes the genetic gain while constraining the rate of inbreeding or the relationships among selection candidates (Wooliams and Meuwissen, 1993; Meuwissen, 1997), and has been extended by Meuwissen and Sonesson (1998) to the case of overlapping generations. Optimum genetic contribution chooses the selected parents and assigns genetic contributions to the next generation for each selected candidate. As an additional tool for specific mating strategies, Sonesson and Meuwissen (2000) developed a simulated annealing algorithm based on OGC results to minimize average inbreeding in the next generation.

The aim of this study was to evaluate the OGC concept for 3 lines of a layer breeding program differing in population size and in the ratio of males to females. Results from OGC were the base for the applied simulated annealing algorithm to define specific matings, which have been compared with breeding strategies of the existing breeding program. Furthermore, the design of the layer breeding program was used to estimate kinship coefficients by applying gene flow theory. To assess the effect of selection on rates of inbreeding, expected results using this novel approach for a random mating system (deterministic as well as stochastic simulation) were compared with increases of inbreeding from real pedigree data.

MATERIALS AND METHODS

Data

Data were from 2 different commercial White Leghorn lines (lines 11 and 22) and from the experimental line 33. Lines 11 and 22 have a similar structure of the breeding program (Figure 1). In total, 60 sires are mated with 600 hens. The program intends to preselect 8 female offspring per mating (4,800 females) and 1 to 3 male offspring per mating (on average 900 males). Performance tests for preselected females are accomplished from wk 20 to 47. The ultimate selection criterion for

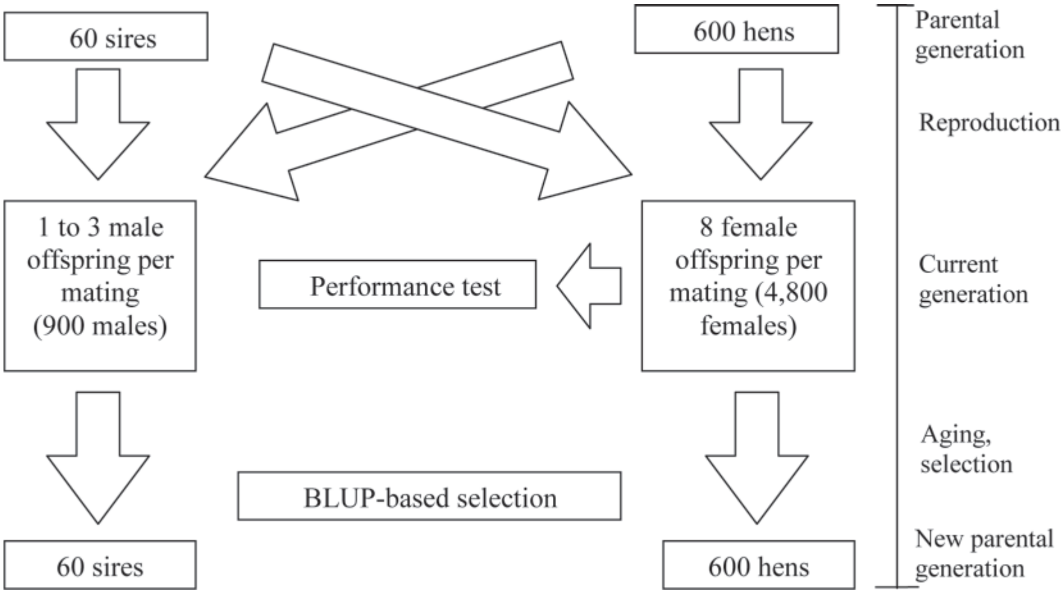

Figure 1. Breeding scheme for the final selection of 60 sires and 600 hens for the commercial large lines 11 and 22. BLUP = best linear unbiased prediction.

females and for males in wk 47 is the BLUP breeding value for egg production. Selection of 60 sires and 600 hens implies replacement rates of 6.7 and 12.5%, respectively. Line 33 is an experimental line that is substantially smaller in population size. Final selection recruits 20 males and 200 females out of 300 performance-tested males and out of 1,600 hens, respectively. However, these theoretical guidelines related to the number of birds used for performance testing and determining the number of selection candidates per year can slightly alter under practical conditions. All selection candidates considered were from the same hatch year. The number of selection candidates was 4,281 (3,283 females, 998 males) for line 11, 4,395 (3,750 females, 645 males) for line 22, and 1,777 (1,542 females, 235 males) for line 33, all having BLUP breeding values for egg production. The pedigree database of selection candidates included 12,357 birds, traced back to hatch year 1995.

OGC Theory

The OGC concept as implemented in the program GENCONT (Meuwissen, 2002) was applied to select males and females with their optimal mating frequencies to breed the next generation. This was done separately within lines. The method implies a maximization of the average genetic merit of the selection candidates, $\mathbf{c}'\mathbf{u}$, by constraining the average relationship, $\mathbf{c}'\mathbf{A}\mathbf{c}$, within this group, where $\mathbf{c}$ is a vector of contributions of each selected animal, $\mathbf{u}$ is a vector of estimated breeding values of selection candidates, and $\mathbf{A}$ is the numerator relationship matrix between selection candidates (Meuwissen, 2002). Hence, a pedigree file is mandatory for the GENCONT program and also is relevant when preparing the additive genetic relationships among selected birds for the simulated annealing algorithm. The parameter file for GENCONT describes the structure of the breeding program. In total, 5 different scenarios for each line were investigated (Table 1). Apart from scenario C, in which the number of offspring per parent was fixed, minimum and maximum genetic contributions of individual sires were defined. Each selected sire was mated with at least 5 hens and with at most 20 hens. Allowing a variation of 5 to 10 selected offspring per mating, at least 25 offspring were from the same selected sire. The maximum contribution was restricted

Table 1. Five scenarios for the GENCONT input parameter file to determine the structure of the breeding program

Scenario	Structure of the breeding program
A	Constraint for additive genetic relationships (a) in the next generation Line 11: $a = 0.151$; line 22: $a = 0.137$; line 33: $a = 0.217$
B	Constraint for increase of inbreeding per generation (ΔF) = 0.01
C	Scenario A + fixing no. of offspring: 5 offspring per hen, 50 offspring per sire
D	Scenario A + selection according to current breeding scheme: 60 males and 600 females for lines 11 and 22; 20 males and 200 females for line 33
E	Constraint for additive genetic relationships (a) in the next generation, being identical to the realized value for a in the practical breeding scheme after 1 round of selection Line 11: $a = 0.132$; line 22: $a = 0.117$; line 33: $a = 0.197$

to 200 offspring per selected sire. The input file also allowed a variation in the number of offspring per selected hen in the range from 5 to 10.

All scenarios were first analyzed without considering the aspect of overlapping generations. Further comparisons considered overlapping generations for males because culling decisions for already used males are based on their genetic values, which can be higher compared with the genetic merit of selection candidates of younger age. Definition of age classes for overlapping generations to determine the gene flow in distinct periods was done according to Meuwissen and Sonesson (1998).

Simulated Annealing Algorithm

After the global determination of genetic contributions of male and female parents by applying the OGC methodology, the simulated annealing algorithm (Press et al., 1992; Sonesson and Meuwissen, 2000) was applied to define the specific matings between hens and sires for the 5 breeding strategies (Table 1). The ultimate goal in this mating tool is to reduce the average inbreeding coefficient in the short-term (i.e., in the following generation). Input parameters included all possible relationships between pairs of selected hens and selected sires. The scheme with the lowest average inbreeding coefficient in the next generation is considered as the optimal one. The essential steps of the algorithm can be summarized as follows: 1) sires and hens are mated at random according to their frequencies in vector **c**, and the resulting average inbreeding coefficient is stored as reference value Z_R; 2) change of mating partners and comparison of the new resulting average inbreeding value Z'_R with Z_R, and 3) for $Z'_R < Z_R$, Z_R is replaced with Z'_R and so forth for all possible matings. By using simulated annealing, inbreeding is avoided as much as possible so that this algorithm ends at a local optimum.

Table 2. Schematic gene flow matrix for the layer breeding program[1]

	Selection group[2]	
Item	SB	HB
SB	1.SB → SB	2.HB → SB
HB	3.SB → HB	4.HB → HB

[1] Arrows indicate the gene flow.

[2] SB = sires in the breeding unit; HB = hens in the breeding unit.

Kinship and Gene Flow Method

The kinship coefficient K_{ij} describes the probability that 2 randomly chosen alleles from the same locus for individuals i and j are identical by descent (Malécot, 1948). The average kinship concept is an extension for the whole genome by including all loci. The analogy between the kinship coefficient and Wright's coefficient of relationship R_{ij} (Wright, 1922) is $K_{ij} = 0.5\ R_{ij}$. Hence, the inbreeding coefficient (Wright, 1922) is equivalent to the coefficient of kinship of the parents. Simianer et al. (2009) developed an approach to estimate kinship coefficients within and between selection groups from gene flow theory (Hill, 1974). Selection groups used for this example for the large lines 11 and 22 were sires in the breeding unit and hens in the breeding unit. Defined selection groups and the schematic gene flow matrix are given in Table 2. The average kinship coefficient F_{ij} between 2 selection groups i and j defines the probability that a randomly drawn allele from locus x in group i and a randomly drawn allele from locus x in group j are identical by descent. Kinship coefficients between and within groups i and j for n_i and n_j individuals, respectively, can be calculated as

$$F_{ij} = \frac{\sum_{k=1}^{n_i}\sum_{l=1}^{n_j} K_{kl}}{n_i n_j} \qquad [1]$$

and

$$F_{ii} = \frac{\sum_{k=1}^{n_i}\sum_{l=1}^{n_i} K_{kl}}{n_i^2}. \qquad [2]$$

Application of formulas [1] and [2] above needs the definition of probabilities of male and female allele origin (i.e., the definition of age classes of parental alleles), the number of animals for each age group, and an indication if individuals within age groups have been generated from reproduction or from aging. These parameters for the layer breeding program for lines 11 and 22 to setting up matrices for reproduction and aging are from Figure 1 [i.e., 900 males are from reproduction (age group 1 = number of reared male chicks), 60 males are from aging due to selection (age group 2), 4,800 hens are from reproduction (age group 3 = number of reared female chicks), and 600 hens are from aging due to selection (age group 4)]. All paternal alleles for males and females in the reproduction matrices have been transmitted from age group 2, whereas the maternal alleles have been received from age group 4. The 60 selected sires and 600 hens are herein after referred to as sires and hens in the aging matrices. This implies a transmission of 100% of paternal and maternal alleles from age group 1 to age group 2 (paternal path of selection) and a transmission of 100% of paternal and maternal alleles from age group 3 to age group 4 (maternal path of selection). To illustrate the effect of intensive selection, the number of selected sires was decreased artificially. This means a reduction of sires in age group 2 to from 60 sires to lower, depicting also the effect of a decreasing effective population size.

RESULTS AND DISCUSSION

OGC and Different Breeding Strategies

Results from OGC for the different breeding strategies stratified by lines are summarized in Table 3. Scenario A (restricting the average relationship among selection candidates) and scenario B (restricting the increase in inbreeding per generation) revealed approximately identical results when evaluating solutions for relationships, the number of selected males and females, and the average genetic value of selected birds. This finding is not surprising because the allowed increase in inbreeding in scenario B (i.e., $\Delta F = 0.01$) corresponds to the constraint for the additive genetic relationships as used in scenario A. However, there are no scientific rules or sophisticated methods for predefining the allowed increase of inbreeding per generation.

Meuwissen and Woolliams (1994) linked effective population size, which is a function of the inbreeding rate, to the decline in fitness of a population. Woolliams et al. (2002) considered the allowed rate of inbreeding per generation as a measure of risk in the economical sense from the perspective of a breeding program. The extra response from higher inbreeding in terms of, for example, higher production in the short-term should compensate inbreeding depressions and the loss of genetic variation in the selected trait.

An additional constraint in scenario C (i.e., fixing the number of offspring per selected sire and hen) was associated with a further loss in genetic gain. The average genetic value of selected birds was 127.9, being substantially lower than average genetic values of 136.9 and 136.8 achieved in scenarios A and B, respectively. Scenario D considered 2 constraints. In addition to the constraint for the additive genetic relationships as used in scenarios A and B, the number of sires and hens for selection was determined in advance. As depicted in Figure 1, exactly 60 sires and 600 hens were selected for lines 11 and 22, and exactly 20 sires and 200 hens were selected for the smaller line 33. The numbers for selected birds are substantially higher compared with values achieved in scenarios A and B, explaining the lower value for additive genetic relationships (0.139 vs. 0.151 and 0.139 vs. 0.150). Scenario E considered a more severe constraint on the allowed relationships compared with scenario A (i.e., 0.139 vs. 0.151). The value of 0.139 corresponds to the value for additive genetic relationships in the next generation, which has been realized in the practical breeding scheme after 1 round of selection. As shown for other species in detail [i.e., dairy cattle (König and Simianer, 2006), pigs (Simianer et al., 2003), horses (Niemann et al., 2009), and beef cattle and sheep (Avendaño et al., 2003)], a decrease of allowed additive genetic relationships was associated with a decrease of the genetic value of 1.5 points. The lower level of relationships has been realized by increasing the number of selected sires (i.e., 60 sires instead of 24 sires, 60 sires instead of 22 sires, or 22 sires instead of 17 sires for lines 11, 22, and 33, respectively). The number of selected hens instead was identical for lines 22 and 33 and was only 1 hen more for line 11 in scenario E. Hence, adaptation to constraints was achieved through a modified selection scheme for sires. This finding is also illustrated in Figure 2 for line 11. The optimal number of sires at each level of the relationship constraint and the corresponding expected genetic gain is depicted for constraints at relationship in the range from 0.10 to 0.16. For the lowest level of the average relationship at 10%, the optimal number

Table 3. Results from optimum genetic contribution application in terms of additive genetic relationships among selection candidates, their average genetic value, and number of selected hens and sires stratified by line

	Additive genetic relationships		Number of selected parents		
Scenario[1]	Constraint	Solution	Sires	Hens	Genetic value
Line 11					
A	0.151	0.151	24	435	136.9
B	0.151	0.150	22	435	136.8
C	0.151	0.136	85	909	127.9
D	0.151	0.139	60	600	131.5
E	0.139	0.139	38	436	135.4
Line 22					
A	0.137	0.134	22	435	135.1
B	0.137	0.135	22	435	135.2
C	0.137	0.122	87	910	127.2
D	0.137	0.125	60	600	130.8
E	0.125	0.125	39	436	134.4
Line 33					
A	0.217	0.217	17	167	130.2
B	0.217	0.217	17	167	130.2
C	0.217	0.191	35	357	122.5
D	0.217	0.207	20	200	127.6
E	0.207	0.207	22	167	129.5

[1] Definitions of breeding scenarios A through E are provided in Table 1.

of sires was 70 and the average genetic value of the selected group was 127.9. At the highest relationship constraint (16%), the optimal number of sires decreased to 15 and the average genetic value increased to 139.7. At the same level of relationship, the mean genetic value of selected parents was 10.9% higher than the results from the conventional selection scheme applied in the practical breeding program.

Hanenberg and Merks (2001) compared results from OGC application with an equal contribution approach in a closed pig breeding program. For the same rate of inbreeding, genetic gain increased by 22% when applying OGC. Hence, OGC is a suitable tool for both reducing inbreeding at a constant genetic progress or increasing genetic gain by keeping inbreeding on a constant level. Meuwissen (1997) and Grundy et al. (1998) applied simulation studies to evaluate OGC theory and they found 20% higher genetic gain when compared with BLUP truncation selection at the same rate of inbreeding.

For small populations or conservation schemes in which the ultimate goal is only focused on reducing inbreeding without maximizing genetic gain, the minimum coancestry or equal contribution of parents is widely recommended (Frankham, 1995). This approach was implemented in scenario C (Table 1), in which each selected sire was used for exactly 11.11% of the matings. For livestock populations that are under selection, optimizing genetic contributions generally means allowing different contributions from different birds as was done in scenarios A, B, D, and E.

OGC and Overlapping Generations

In the context of animal breeding, the expression overlapping generations implies mating systems in which more than one breeding generation is present at a given time. When generations overlap, some parents have been considered in mating designs in previous rounds of selection and already produced offspring. The opposite refers to discrete generations, in which selected animals produce offspring and are culled afterward. This is the typical mechanism in fish or poultry breeding (Rutten et al., 2002) and is fully considered when applying dynamic selection rules (Wray and Goddard, 1994; Brisbane and Gibson, 1995). In general, overlapping generations are not generally taken into account in poultry research or in applied poultry breeding (Gowe and Fairfull, 1990), although the idea for considering overlapping generations as implemented in GENCONT (Meuwissen and Sonesson, 1998) may have practical relevance for a commercial poultry breeding program.

The comparison of OGC results with and without overlapping generations was done for the practical standard breeding program (i.e., scenario D) for lines 11, 22, and 33. Only minor differences in terms of solutions for additive genetic relationships and genetic merit were found (Table 4). This finding implies that breeders have been replaced by their progeny and were not used for several rounds of matings. Another argument when receiving the same solutions with and without considering overlapping generations is the reduction in the required computing time. Press et al. (1992) and Meuwissen and Sonesson (1998) showed that the computing time largely depends on the number of selection candidates due to matrix inversions required to calculate the optimal contributions. In addition, we found a 3 times longer computing time when considering overlapping generations. For short intervals of selection, and identical results as found in this evaluation, there is no necessity to use overlapping generations.

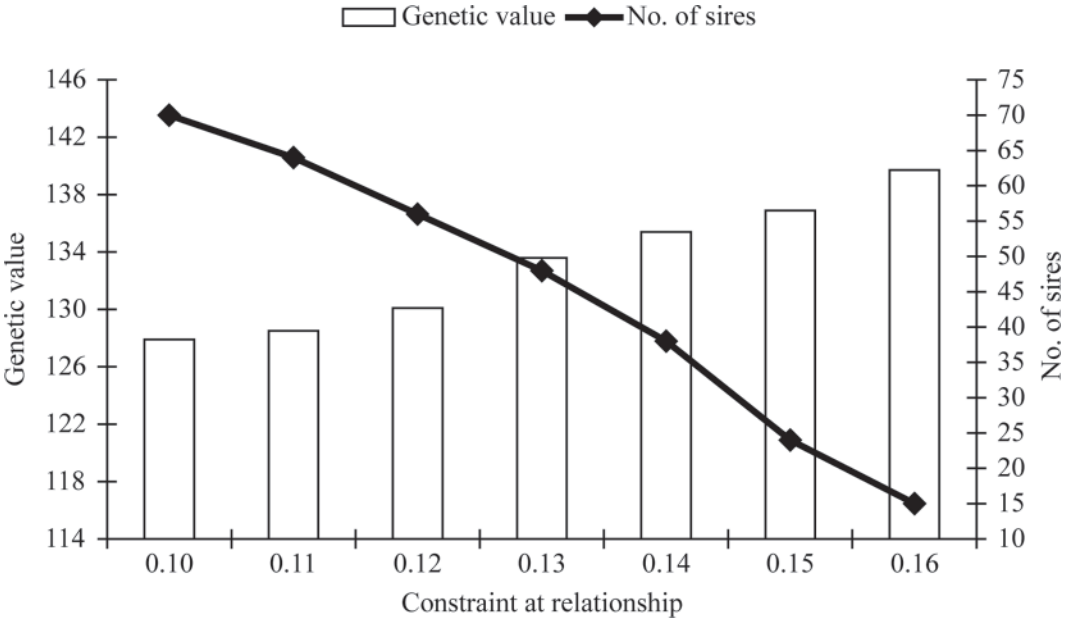

Figure 2. Genetic value of selected birds and number of selected sires at different constraints for average relationships (line 11, scenario A).

Table 4. Comparison of solutions for additive genetic relationships and genetic merit of selected parents when applying optimum genetic contribution with (yes) and without (no) overlapping generations for scenario D stratified by lines

	No. of selected parents		Additive genetic relationships		Genetic merit	
Line	Sires	Hens	Yes	No	Yes	No
11	60	600	0.139	0.139	131.57	131.54
22	60	600	0.125	0.125	130.83	130.82
33	60	600	0.207	0.207	127.55	127.55

Specific Mating Plans

Using the solutions of genetic contributions from OGC, the ultimate goal in this mating tool is to reduce the average inbreeding coefficient in the short-term in the following generation (Sonesson and Meuwissen, 2000). Additional input parameters considered all possible relationships between pairs of selected sires and selected hens. These relationships were calculated by applying CFC software (Sargolzaei et al., 2006). Specific mating plans using this simulated annealing algorithm were developed for breeding scenarios A, B, C, D, and E, stratified by lines. The algorithm provides a mating plan with an average coefficient of relationships for matings that are substantially lower than when they are compared with the average relationships obtained from all possible matings of OGC-selected birds (Table 5). The reduction of the average additive genetic relationships for all of the matings was in the range from 32.8% (scenario A, line 22) up to 44.9% (scenario D, line 33).

For another comparison, the same number of sires and hens was used for the simulated annealing algorithm, but the sires and dams were randomly mated. This resulted in a substantially higher coefficient of relationship (i.e., up to 8.7% for scenario D in line 33). The reduction in genetic relationships when applying the simulated annealing algorithm was mainly due to the elimination of extremely high relationships between hens and sires. The highest values for the coefficients of relationships when considering all possible matings were 0.64, 0.60 or 0.63, and 0.68 for lines 11, 22, and 33, respectively (Table 5). But when focusing only on inbreeding minimization in the next generation, those matings having the highest relationships were not considered in the specific mating plan. The algorithm enabled mating plans with average coefficients of relationship reduced by almost 50%.

Direct advantages in terms of genetic gain and relationships between matings when applying OGC theory in combination with simulated annealing in practical breeding programs are illustrated in Figure 3. For this comparison (i.e., OGC results vs. parameters of the existing breeding scheme), results from OGC scenario E were used. In scenario E (Table 1), the constraint for additive genetic relationships in the next generation is identical to the realized value in the existing breeding program after 1 round of selection. Average genetic val-

Table 5. Additive genetic relationships between sires and hens for all combinations of optimum genetic contribution-selected birds (all) and for the specific matings when applying the simulated annealing algorithm (mate)

			Additive genetic relationships for matings					
	No. of matings		Mean		Minimum		Maximum	
Scenario[1]	All	Mate	All	Mate	All	Mate	All	Mate
Line 11								
A	10,440	435	0.129	0.082	0.054	0.056	0.641	0.110
B	9,570	435	0.131	0.082	0.051	0.056	0.641	0.119
C	77,265	909	0.131	0.083	0.048	0.054	0.641	0.118
D	36,000	600	0.132	0.084	0.051	0.059	0.641	0.113
E	16,568	436	0.127	0.078	0.053	0.056	0.641	0.111
Line 22								
A	9,570	435	0.119	0.080	0.022	0.052	0.595	0.108
B	9,570	435	0.121	0.080	0.022	0.052	0.595	0.119
C	79,170	910	0.119	0.074	0.039	0.047	0.629	0.110
D	36,000	600	0.120	0.076	0.022	0.050	0.629	0.106
E	17,004	436	0.114	0.073	0.022	0.052	0.595	0.102
Line 33								
A	2,839	167	0.187	0.105	0.067	0.067	0.678	0.153
B	2,839	167	0.187	0.105	0.067	0.067	0.678	0.153
C	12,459	357	0.185	0.104	0.060	0.068	0.678	0.164
D	4,000	200	0.185	0.102	0.065	0.068	0.678	0.157
E	3,674	167	0.183	0.103	0.065	0.069	0.678	0.153

[1] Definitions of breeding scenarios A through E are provided in Table 1.

ues of OGC-selected birds were 135.4 for line 11, 134.4 for line 22, and 129.5 for line 33. Genetic values from the existing breeding program were lower (i.e., 131.0, 129.2, and 128.5 for lines 11, 22, and 33, respectively). The OGC preselection of parents combined with the simulated annealing algorithm also resulted in a decrease of additive genetic relationships between mating pairs when compared with the existing breeding program. The decrease was 0.025 for line 11, 0.019 for line 22, and 0.095 for line 33. Hence, OGC in combination with the specific mating tool shows potential for an increase of genetic gain by reducing inbreeding in the next generation for the current poultry breeding program. The highest differences between theoretical expectations and practical results in terms of genetic relationships were found for line 33. However, line 33 is not used in a commercial context but rather should be considered as a reserve population. This definition of line 33 can partly explain some of the large differences between practical parameters and the theoretical potential.

The results from the simulated annealing algorithm are also in agreement with calculations conducted in a Holstein dairy cattle population (König and Simianer, 2006). As one example from this study, 21 selected bull sires and 30 bull dams mated at random resulted in an expected inbreeding coefficient for their progeny of 1.38%. The simulated annealing algorithm suggested a mating plan with an average inbreeding coefficient of only 0.46%. The simulated annealing algorithm can be considered as a strategy for avoiding or minimizing inbreeding in the short-term. The application makes sense for such species characterized by long generation intervals (e.g., dairy cattle). For short generation intervals as prevalent in poultry breeding, the advantage of minimizing inbreeding in the short-term will erode very quickly. These circumstances were illustrated by Simianer et al. (2003). For a closed population without gene transfer from outside and short generation intervals, the most promising breeding strategy for finding the balance between inbreeding and genetic gain is to apply OGC but afterward to use random matings of selected males and females.

Theoretical Kinship from Gene Flow Theory

Expansion of the average kinship within and between defined age groups under a random mating system from the deterministic approach is shown in Figure 4. Kinship coefficients for male and female selection groups are identical because maternal and paternal alleles of birds within these groups have an identical origin (i.e., are inherited from the same matings). Kinship coefficients in groups 2 and 4 generated from aging do follow the kinship coefficients in groups 1 and 3, respectively, with a time lag of 1 generation. The average increase of the kinship coefficient is 0.11% per generation for all defined selection groups. Results from this deterministic approach are in accordance with results from a stochastic simulation under a random mating system [i.e., 0.10% for group 1 (males from reproduction), 0.17% for group 2 (males from aging), 0.11% for group 3 (hens from reproduction), and 0.14% for age group 4 (hens from aging)].

As explained before, the inbreeding coefficient of an individual (Wright, 1922) is equivalent to the coefficient

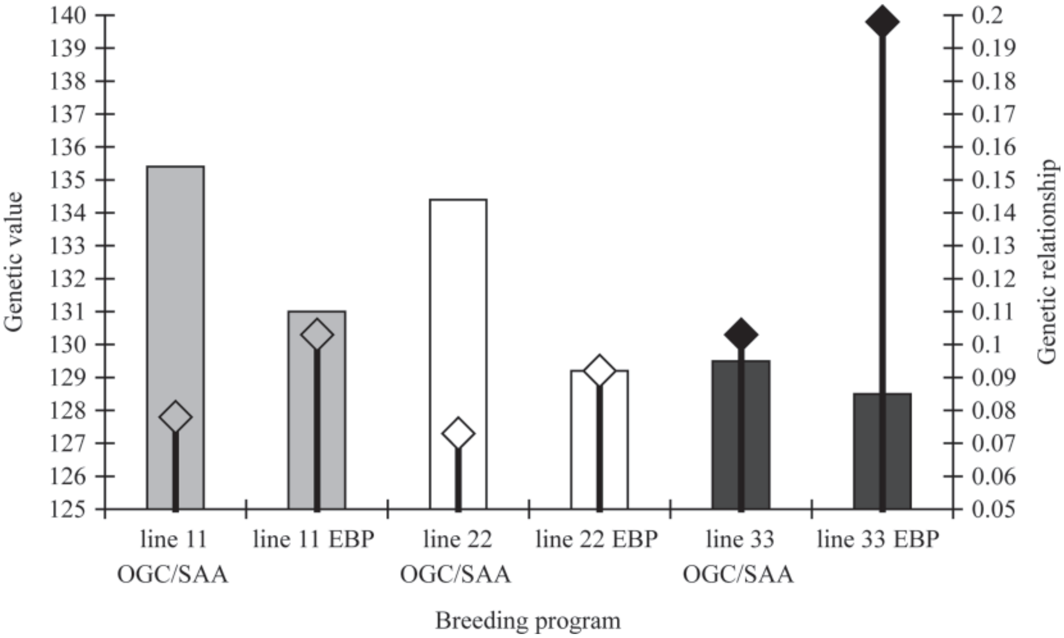

Figure 3. Comparison of genetic values (bars) of selected birds from optimum genetic contribution (OGC) application (scenario E) and of the additive genetic relationships (rhombs) between mating partners after applying the simulated annealing algorithm (OGC/SAA) with the corresponding parameters of the existing poultry breeding program (EBP) stratified by lines.

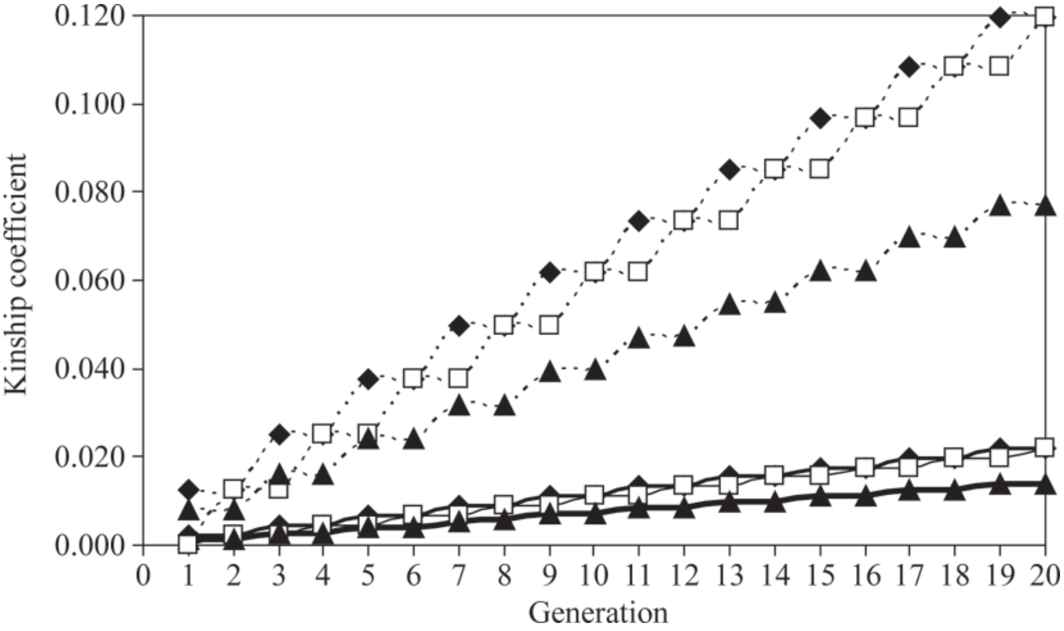

Figure 4. Average kinship coefficients estimated from gene flow theory (deterministic approach) within groups generated from reproduction (black rhombs), within groups generated from aging (white squares), and between groups (black triangles) for generations 1 to 20 (solid lines: according to the current selection scheme for 60 sires per generation as outlined in Figure 1; dotted lines: artificial selection scheme for 10 sires per generation).

of kinship of the parents. However, there is a substantial difference when comparing the development of kinship coefficients from the theoretical approach (0.1%) with increases of inbreeding per generation from real pedigree data (0.9%). This difference implies that intensive selection, as applied in poultry breeding, has tremendous effect on the rate of inbreeding and has a further consequence on effective population size. An artificial reduction of the number of selected sires from 60 to 10 leads to an increase of inbreeding per generation being identical to the results obtained from the pedigree-based approach (Figure 4, dotted lines). Bijma et al. (2001) presented a general approach, also based on gene flow theory, to calculate rates of inbreeding for typical livestock improvement schemes. For such practical breeding schemes, predictions for the increase of inbreeding obtained from their method were substantially more accurate compared with other approaches ignoring the effect of selection. Tsehay (2005) used simulations to compare the inbreeding coefficient for different mating systems in layers. The average inbreeding coefficient for assortative matings was 91% higher compared with the value from a random mating system. The effect of selection on rates of inbreeding can also be demonstrated when comparing results from pedigree data to the theoretical expectations from gene flows for populations undergoing random matings as done in our present study. Large differences in rates of inbreeding when comparing expected results from a random mating system to values that have been realized in practice underline the necessity to establish selection tools considering both aspects of long-term relationships and genetic gain.

Suggestion for Practical Application

Optimal genetic contribution theory in combination with the simulated annealing algorithm to create specific matings has been proven to be an adequate mechanism to manage genetic relationships in the long and inbreeding in the short perspective in layer populations. This study shows that the application of dynamic optimization tools allows the management of genetic relationships with additional potential for increasing genetic gain. Furthermore, OGC can be successfully used for conservation schemes or for the breeding of reserve populations (e.g., the experimental line 33). For such schemes, the primary goal is to minimize the inbreeding rate while achieving a predefined level of genetic gain. Furthermore, OGC allows a flexible mating ratio instead of fixed presettings. Based on the increased availability of molecular markers of different types, several approaches for the management of inbreeding using molecular markers in combination with pedigree information have been suggested (Wang, 2001). However, those sophisticated ideas mainly have been evaluated in simulation studies. The OGC has been carefully analyzed using both simulation techniques (Sonesson and Meuwissen, 2002) and data from practical breeding programs as was done in this study. Due to the advantages of OGC over traditional breeding policies, OGC has been implemented in practical dairy cattle (Weigel and Lin, 2002) and in practical pig breeding programs (Luther and Hofer, 2006). Due to the potential of OGC in terms of genetic gain and genetic relationships over conventional breeding strategies as shown in our study, its application is also strongly recommended for the management of inbreeding in poultry populations.

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