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Expected increases in genetic merit from using optimized contributions in two livestock populations of beef cattle and sheep¹

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ABSTRACT: The expected benefits from optimized selection in real livestock populations were evaluated by applying dynamic selection algorithms to two livestock populations of sheep (Meatline) and beef cattle (Aberdeen Angus). In addition, the effects of introducing BLUP evaluations on the population structure, genetic gain, and inbreeding were investigated. The use of BLUP-EBV accelerated the rates of gain in the Meatline, but the effects of BLUP evaluations on Aberdeen Angus are not as evident. Although steady increases in the average coefficient of inbreeding (F) were observed, the inbreeding rates (ΔF) before and after the introduction of BLUP evaluations were not significantly different. The observed ΔF in the last generation was 1.0% for Meatline and 0.2% for Aberdeen Angus. The applica-

tion of the dynamic selection algorithms for maximizing genetic gain at a fixed ΔF led to important expected increases in the rate of genetic gain (ΔG). When ΔF was restricted to the value observed in both populations, increments per year in ΔG of 4.6 (i.e., 17%) index units for Meatline and 3.5 (i.e., 30%) index units for Aberdeen Angus were found in comparison to the ΔG expected from conventional truncation BLUP selection. More relaxed constraints on ΔF allowed even higher expected increases in ΔG in both populations. This study demonstrates that the optimization tools constitute a potentially highly effective way of managing gain and inbreeding under a broad range of schemes in terms of scale and inbreeding level. No losses in genetic gain were associated with the use of dynamic optimization selection when schemes were compared at the same ΔF .

Key Words: Beef Cattle, Genetic Gain, Inbreeding, Optimization, Sheep

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Introduction

Best linear unbiased prediction (BLUP) has become the standard method for genetic evaluation in breeding programs of beef cattle and sheep livestock populations. Although selection exclusively based on BLUP EBV allows accurate selection and increased genetic

gains, it can also lead to increased rates of inbreeding in comparison with less accurate methods (e.g., Quinton et al., 1992).

Although inbreeding is unavoidable in closed selection programs, increases in inbreeding need to be restricted to alleviate long-term negative effects (Lamberson and Thomas, 1984; Burrow, 1993). Woolliams et al. (2002) have described the rate of inbreeding as a measure of risk from the perspective of the breeding program justifying its management with arguments that go beyond avoiding inbreeding depression and loss of genetic variation in the selected trait.

Dynamic tools for maximizing genetic progress while constraining the rate of inbreeding to a predefined value are now available (Meuwissen, 1997; Grundy et al., 1998; Meuwissen and Sonesson, 1998; Grundy et al., 2000). These tools optimize the number of parents and their contributions to subsequent generations for maximizing gain for a fixed rate of inbreeding. Simulation studies showed improvements in genetic gain greater than 20% over BLUP truncation selection at the same rate of inbreeding (Meuwissen, 1997; Grundy et al., 1998). However, the expected ben-

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efits from optimized selection in real livestock populations remain unknown.

The main objective of this study was to evaluate the potential extra gains to be obtained by dynamic optimization algorithms in two livestock populations of sheep (Meatline) and beef cattle (Aberdeen Angus). This was accompanied by a description of the population structure and rates of genetic gain and inbreeding before and after the introduction of BLUP evaluations. Relationships between contributions of ancestors of the current populations and their EBV were also evaluated.

Materials and Methods

The Meatline and Aberdeen Angus breeds were chosen for this study because they have maintained effective improvement programs and have achieved high genetic gains in the United Kingdom when compared with other breeds of sheep and beef cattle, respectively (Simm, 1998; M.L.C., 1999). Also, in both populations, concerns regarding increasing levels of inbreeding and its potential consequences have arisen (G. Nieuwhof, personal communication, M.L.C., Milton Keynes, U.K.).

Data

The Aberdeen Angus is a traditional British beef breed, with a recorded pedigree extending over 50 yr. The Meatline is a synthetic terminal sire breed of sheep created in the United Kingdom in the early 1960s. In contrast with Aberdeen Angus, the recorded Meatline pedigree is relatively small, covering only 24 yr. Pedigree data and index scores for both populations were provided by the Meat and Livestock Commission (M.L.C., Milton Keynes, U.K.). The two indices provided were the BLUP-EBV for the breeding goals of U.K. terminal sire breeds of beef cattle and sheep ("beef value" and the "lean index," respectively). The beef value includes carcass weight, carcass conformation score, and carcass fat score (Amer et al., 1998; Simm, 1998), whereas the lean index includes carcass lean weight and carcass fat weight (Simm and Dingwall, 1989).

The Aberdeen Angus pedigree included a total of 119,953 animals (57,431 males and 62,522 females) born from 1948 to 2000. A total of 45,472 parents (6,686 sires and 38,786 dams) were identified. The Meatline pedigree included a total of 12,391 animals (5,661 males and 6,730 females) born from 1974 to 2000. A total of 3,742 parents (329 rams and 3,413 ewes) were identified. Parents with unknown genealogies were considered as "base parents." This group represented 28.9% of the total number of parents (2,443 sires and 10,704 dams) in Aberdeen Angus and 7.4% of the total number of parents (35 rams and 243 ewes) in Meatline.

Because multitrait BLUP evaluations were introduced for both populations in 1991, the analyses per-

formed were each applied to three periods of data. The three periods included an overall period covering all years with available information, and two periods of approximately equal length defined pre-BLUP and post-BLUP introduction.

Generation Intervals

The generation interval for each breed was computed as the average age of parents at the birth of their offspring. It was calculated for each year of birth and then averaged over years for all parents (L), for sires (L_m), and for dams (L_f).

Rates of Genetic Progress and Inbreeding

Average index scores and inbreeding coefficients of individuals born at each year were calculated. The inbreeding coefficients (F) were obtained from the additive relationship matrix that was computed using the algorithm of Meuwissen and Luo (1992). The rate of genetic gain (ΔG) and the rate of inbreeding (ΔF) were computed as the linear regression of the average index score and average F on the year of birth, respectively.

Both ΔG and ΔF were analyzed for the three periods in both populations. For Meatline, the periods were 1) overall period from 1974 to 2000, 2) pre-BLUP period from 1983 to 1991, and 3) post-BLUP period from 1992 to 2000. For Aberdeen Angus, the corresponding periods were 1) overall period from 1948 to 1999, 2) pre-BLUP period from 1983 to 1991, and 3) post-BLUP period from 1992 to 1999.

Long-Term Genetic Contributions

The effect of different cohorts of ancestors on genetic gain was investigated by studying the relationship between their long-term genetic contributions and index scores. The long-term contribution (r) of an ancestor is defined as the proportion of genes it contributes over the long term to the population (Wray and Thompson, 1990). Over many generations, in a population thoroughly mixed, the r of an ancestor will converge to the same value for all of its descendants but will differ among ancestors (Woolliams et al., 1999). Long-term contributions were computed following the approach used by Woolliams and Mäntysaari (1995). To compute r , a generation of ancestors and a generation of descendants were defined according to average generation intervals previously calculated. Thus, the ancestral and descendant generations were defined by using L . This definition ensures that r summed over all ancestors over a period of L yr equals unity (Bijma and Woolliams, 1999). Convergence of contributions was assumed if the variance of contributions of ancestors across descendants was lower than 1.0×10^{-4} . For Meatline (where L was about 2 yr), contributions were calculated for two generations of ancestors: a) the cohorts born between 1983 and 1984 and b) the cohorts

born between 1991 and 1992 (i.e., the first generation after the introduction of BLUP evaluation). For both groups of ancestors, descendants were the cohorts born between 1999 and 2000. For Aberdeen Angus, ancestors were the cohorts born between 1976 and 1979 (L was about 4 yr from 1971 to 1988), and the descendants were the cohorts born between 1995 and 1999 (L was about 5 yr from 1988 to 2000). The regression of the long-term genetic contribution of ancestors on their index scores was calculated for each cohort of ancestors.

Optimizing Genetic Contributions for Maximizing Genetic Gain

The potential extra genetic gains expected from using selection tools based upon the algorithm described by Meuwissen (1997) were investigated. The algorithm was used to obtain the number of individuals to be selected and the number of offspring each of them should contribute to the next cohort, to achieve the maximum ΔG while constraining ΔF to a specific value. Different restrictions on ΔF were considered. The algorithm maximized the following objective function (Meuwissen, 1997):

$$H_t = \mathbf{c}_t^T \mathbf{g}_t - \lambda_0(\mathbf{c}_t^T \mathbf{A}_t \mathbf{c}_t - C_t) - [\mathbf{c}_t^T \mathbf{Q} - (1/2)\mathbf{1}^T]\lambda$$

where \mathbf{c}_t is the solution vector of mating proportions (c) of candidates at generation t , \mathbf{g}_t is the vector of EBV of selection candidates, \mathbf{A}_t is the numerator relationship matrix for selection candidates, \mathbf{Q} is a known incidence matrix for the sex of the candidates, $\mathbf{1}^T$ equals [1 1], and λ_0 and λ are Lagrangian multipliers. The restriction on the inbreeding rate was achieved each generation by setting $C_t = 2[\Delta F + (1 - \Delta F)F_t]$, where F_t is the average inbreeding coefficient of selection candidates. The third term in the objective function ensures that male and female parents contribute with a half of the gene pool each. Selected candidates are those with $c > 0$ and will contribute to the next generation according to their c value.

The optimization described above does not take into account any constraint on the maximum contribution a particular candidate may have that may arise from reproductive limitations. This might not be a problem in males since AI techniques are often widespread in livestock populations. However, it can be unrealistic for female candidates for which high reproductive rates are less feasible, particularly in beef cattle and sheep populations. In order to obtain more-realistic results, another set of optimizations was run with an additional constraint on the female contributions. In this case, all females were selected by setting their contributions to a predefined value (i.e., $1/2n_f$, where n_f is the number of female candidates). This implies that all female candidates are selected and only male mating proportions are optimized. The objective function was modified following Meuwissen (1997, Appendix):

$$H_t = \mathbf{c}_t^T \mathbf{g}_t - \lambda_0(\mathbf{c}_t^T \mathbf{A}_{11_t} \mathbf{c}_t + 2\mathbf{c}_t^T \mathbf{A}_{12_t} \mathbf{c}_2 - K_t) - (\mathbf{c}_t^T \mathbf{Q}_1 - \mathbf{s}^T)\lambda$$

where \mathbf{c}_t is the solution vector of mating proportions of male candidates at generation t ; \mathbf{g}_t is the vector of EBV of male candidates; \mathbf{A}_{11_t} and \mathbf{A}_{12_t} are submatrices of \mathbf{A} including only male, and male by female candidates, respectively; \mathbf{c}_2 is the known vector of female mating proportions; K_t is $2C_t - \mathbf{c}_2^T \mathbf{C}_2$; \mathbf{A}_{22_t} is the relatedness matrix for female candidates; \mathbf{s}^T is a vector with constant values [0 1/2]; and \mathbf{Q}_1 is a known incidence matrix for males analogous to \mathbf{Q} in the unconstrained case. Software was developed in Fortran 90 to solve the objective functions described above.

Potential benefits from using optimized contributions were estimated by comparing the expected index gains obtained by using the selection algorithm after mimicking selection in 1999 to 1) the actual observed ΔG in 2000 and 2) the expected ΔG in 2000 under truncation selection (i.e., equal contributions) at the observed ΔF in the population being evaluated. The expected ΔG from truncation selection was calculated by allocating a fixed mating proportion to female candidates (i.e., equivalent to one mating) and by selecting the number of male candidates that gave the observed ΔF . This latter comparison allows evaluating the expected benefits from optimizing contributions independently to the benefits of selecting solely on the index. The fact that in practice selection intensity might be lower than that achievable if selection decisions include criteria other than exclusively BLUP-EBV (e.g., Lewis and Simm, 2000) is not accounted for in the first comparison.

Candidates for the selection algorithms were defined by using both L_m and L_f . Therefore, for Meatlinec, candidates were those males born in 1999 ($L_m = 1.0$ yr) and those females born from 1996 to 1998 inclusive ($L_f = 3.0$ yr). The total number of candidates was 1,841. For Aberdeen Angus, candidates were those males and females born from 1992 to 1998 inclusive ($L_m = L_f = 5.0$ yr) and this gave a total number of candidates of 55,553. However, in order to reduce computing requirements, a preselection of candidates was performed by imposing a minimum index score. For Meatlinec, 1,297 candidates (395 males and 902 females) with index score equal to or greater than 179.0 were included. For Aberdeen Angus, 6,429 candidates (3,321 males and 3,108 females) with index score equal to or greater than 21.0 were included. When only male mating proportions are optimized, computer requirements were higher and, in this case, only 417 male candidates (those with index score equal to or higher than 30.0) were included in the Aberdeen Angus optimization. The index scores were those obtained from the M.L.C. genetic evaluation in 2000, and ΔF was constrained to a range of values including the observed inbreeding rate per generation in each breed.

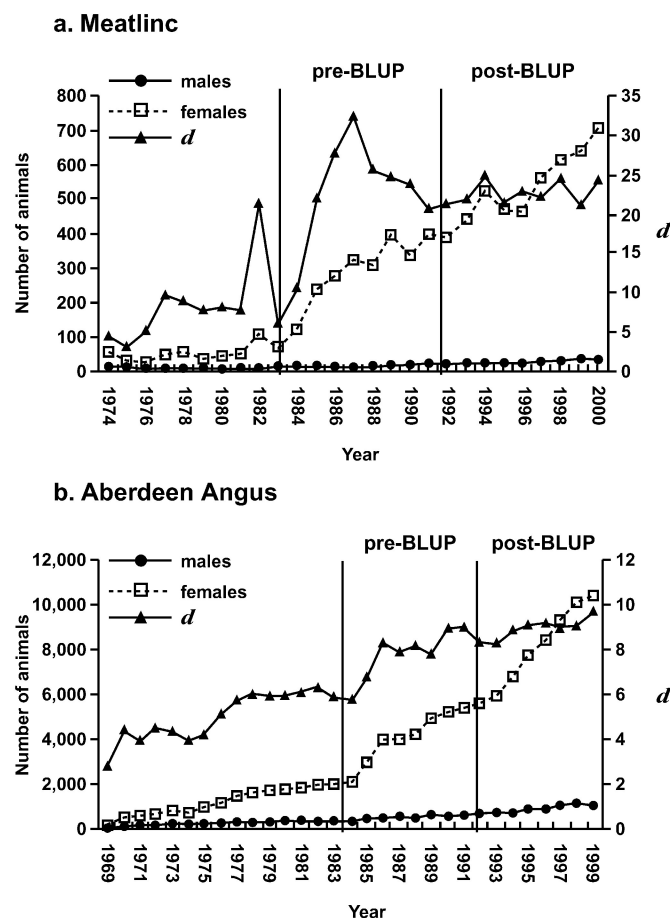


Figure 1. Number of male and female parents and ratio dams to sire (d) across years for Meatlinec (1974 to 2000) and Aberdeen Angus (1969 to 1999). The pre- and post-BLUP periods are indicated.

Results

The pre- and post-BLUP periods are indicated in the figures presenting results on population structure (Figure 1), generation intervals (Figure 2) and rates of genetic gain and inbreeding (Figure 3). The total number of years analyzed in each case depended on the available information, but the pre- and post-BLUP periods are indicated according with the definition given in the Methods section.

Population Structure

Table 1 shows descriptive statistics summarizing the population structure for both populations. The number of Meatlinec rams and ewes, and the ewe-to-ram ratio (d) per year are shown in Figure 1a for the period 1974 to 2000. A large increase in the number of ewes per ram was observed from 1974 ($d = 4.5$) to 2000 ($d = 24.4$), although the ratio remained more or less constant for the period after the introduction of BLUP. The breed showed an important expansion through a steady increase in the number of ewes from

Table 1. Summary of females-to-males ratio (d), number of offspring per male and female parent, and generation intervals (L for overall; L_m for males and L_f for females) for Meatlinec and Aberdeen Angus

Parameter	Meatlinec	Aberdeen Angus
d^a	17.7	6.8
Offspring/male		
25 to 75% range	27–43	2–19
Average	37.6	18.4
SD	23.7	49.1
Maximum	164	1,093
Offspring/female		
25 to 75% range	2–4	2–6
Average	3.6	3.2
SD	2.6	1.6
Maximum	21	42
L^b	2.15	5.09
L_m	1.08	4.95
L_f	3.22	5.24

^aThe average d was calculated from 1974 to 2000 for Meatlinec and from 1969 to 1999 for Aberdeen Angus.

^bThe average L was calculated from 1983 to 2000 for Meatlinec and from 1976 to 2000 for Aberdeen Angus.

1981, from about 50 to about 700 in 2000. The increase in the number of rams was, however, moderate from about 5 in 1974 to about 30 in 2000.

For Aberdeen Angus, a steady increase in the number of dams per sire was observed from 1969 ($d = 2.8$) to 1999 ($d = 10$) (Figure 1b). The number of breeding animals increased substantially from 1984, particularly the number of dams, which showed a fivefold increase. In contrast with the Meatlinec case, this might be due to an increase in the breed membership to the recording services rather than to a genuine breed expansion.

The average number of offspring per male across year in Aberdeen Angus (18.4) was very close to the upper bound of the 25% to 75% interquartile range (2 to 19; Table 1), indicating a much more skewed distribution than for Meatlinec, where the average (37.6) falls near the mid-point of the range (27 to 43; Table 1).

Generation Intervals

Figure 2 shows the average generation interval over years for males (L_m) and females (L_f) for Meatlinec and Aberdeen Angus. In Meatlinec, L_m was calculated from 1983 onward because ram dates of birth were not available before that year. An important increase in L_f over years was observed in the period 1976 to 1983. This increase is related to the period of establishment of this synthetic breed in which females had to be kept in the flock for more time. From 1984 onward, L_f remained unchanged and the average was 3.2 yr. In this population, L_m remained unchanged around a value

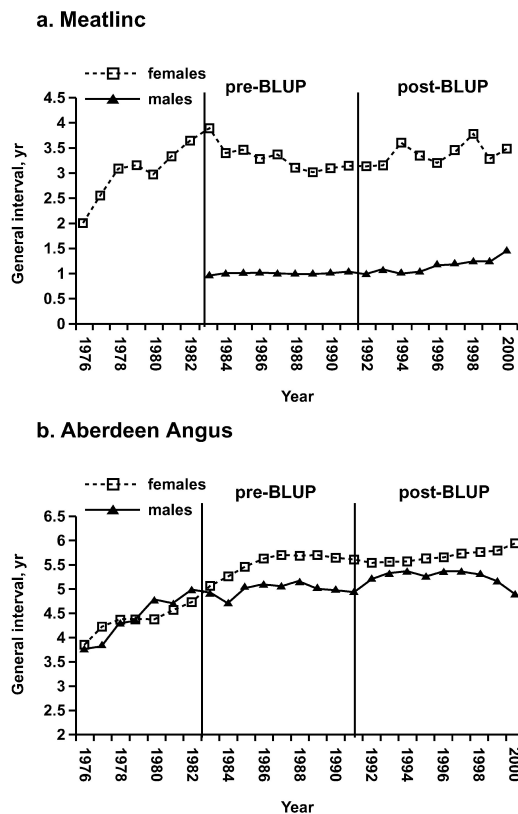


Figure 2. Male and female average generation intervals across years for Meatlinic (1976 to 2000) and Aberdeen Angus (1976 to 2000). The pre- and post-BLUP periods are indicated.

of 1.0 yr over the pre-BLUP period but has slightly increased over the post-BLUP period up to 1.4 yr.

In Aberdeen Angus both L_m and L_f increased at similar rates (0.11 ± 0.02 and $0.16 \pm 0.01/\text{yr}$, respectively) during the period 1976 to 1987 (Figure 2b). The average L_m and L_f in this period were 4.6 and 4.7 yr, respectively. Over the last 12 analyzed years (1988 to 2000), L_m and L_f averaged 5.2 and 5.7 yr, respectively, although since 1994 the generation intervals started to diverge. By the year 2000, L_f was around 1 yr larger than L_m . There was no evidence to link this increase in L_m and the use of BLUP-EBV.

Rates of Genetic Progress

Figure 3 shows the average index values per year of birth for Meatlinic and for Aberdeen Angus for the periods 1982 to 2000 and 1970 to 1999, respectively. Results indicate that the introduction of BLUP evaluations led to a sustained increase in the rate of genetic gain in Meatlinic from 1994. The difference between ΔG in the pre- and post-BLUP periods was statistically significant. For this breed, ΔG was 5.5 ± 1.0 ($P < 0.01$) index units per year in the pre-BLUP period, and 16.5 ± 0.6 ($P < 0.01$) index units per year in the post-BLUP

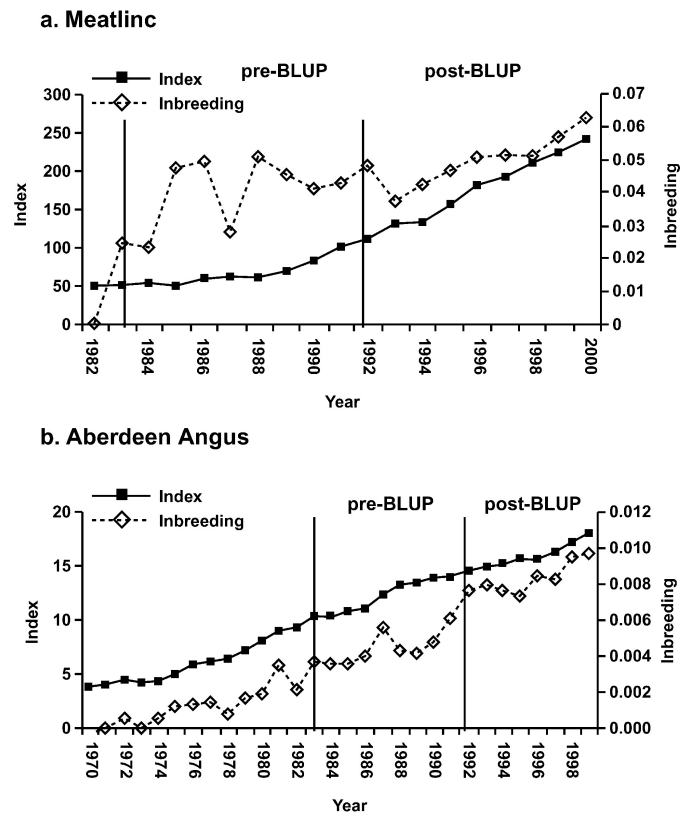


Figure 3. Average index score and inbreeding coefficient across years for Meatlinic (1982 to 2000) and Aberdeen Angus (1970 to 1999). The pre- and post-BLUP periods are indicated.

period. On the other hand, the ΔG for Aberdeen Angus before and after the BLUP introduction were not significantly different. The pre-BLUP and post-BLUP rates of gain were 0.55 ± 0.04 ($P < 0.01$) and 0.46 ± 0.05 ($P < 0.01$) index units per year, respectively.

Rates of Inbreeding and Long-Term Contributions

The average inbreeding coefficient (F) in the Meatlinic population in 2000 was 6.3% (Figure 3a). The ΔF per year for the period 1982 to 2000 was 0.19% ($P < 0.001$). The difference between ΔF in the pre- and post-BLUP periods, $0.21\% \pm 1.31\%$ and $0.23\% \pm 0.05\%$, respectively, was not significant. Nevertheless, the pre-BLUP estimation of ΔF should be taken with caution because F fluctuated considerably in this period. Considering that the generation interval of the population in the post-BLUP was about 2.3 yr (Figure 2a), the ΔF per generation in this period was 0.53%. This is equivalent to an effective size of the population (N_e) of 95 animals (i.e., $N_e = 1/\Delta F$). On the other hand, the ΔF increased in the last generation up to about 1.0% (i.e., $N_e = 50$).

The average F in the Aberdeen Angus population in 1999 was about 0.97% (Figure 3b). For the period 1974

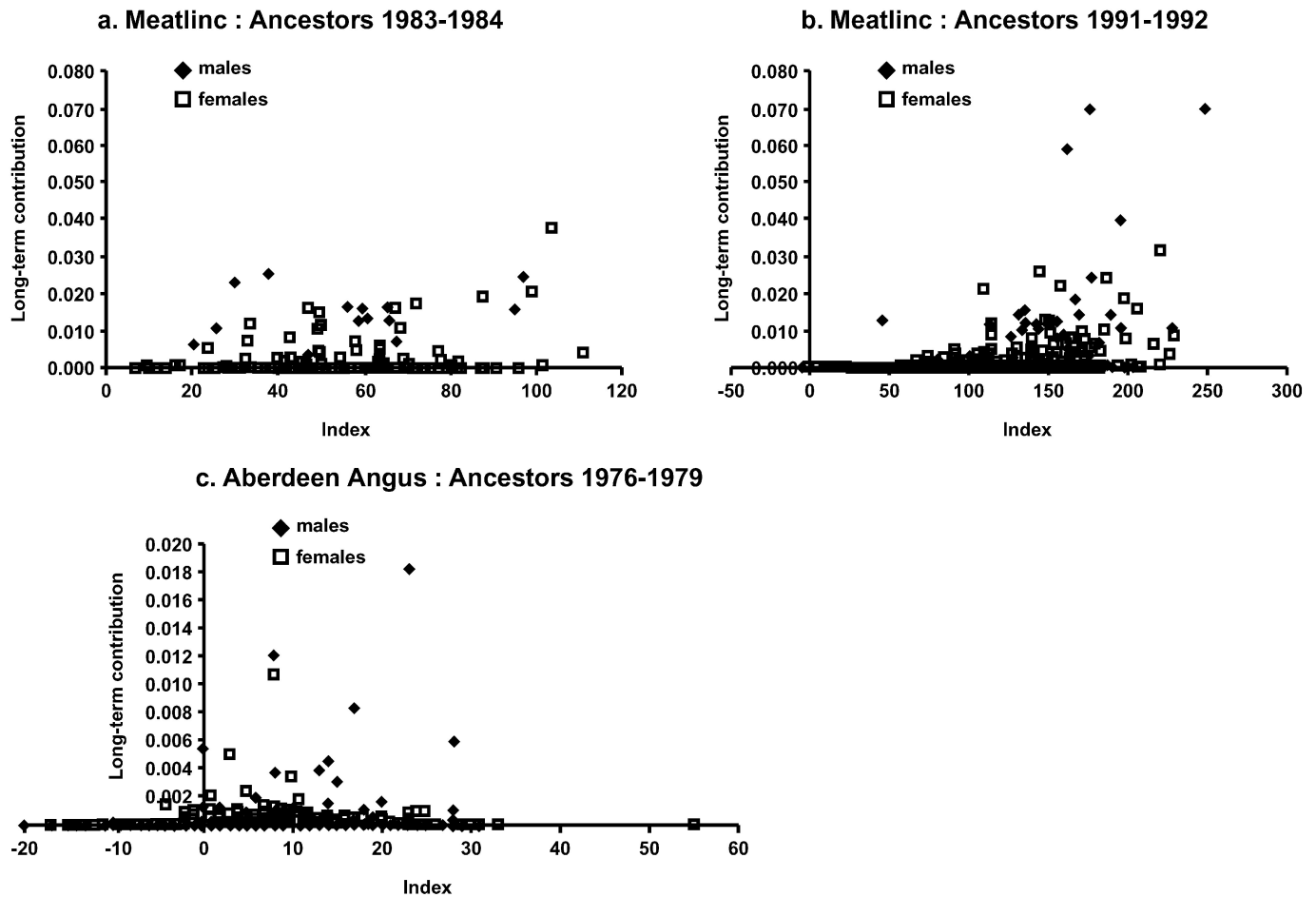


Figure 4. Relationship between long-term genetic contributions and index scores of selected male and female ancestors for Meatlinec and Aberdeen Angus.

to 1999, ΔF was 0.04% per yr ($P < 0.001$). As with Meatlinec, the rate of inbreeding for the pre- and post-BLUP periods were similar ($0.02\% \pm 0.008\%$ and $0.03\% \pm 0.008\%$, respectively). Considering that the generation interval was about 5 yr (Figure 2b), ΔF per generation in the post-BLUP period was approximately 0.15% (i.e., $N_e = 333$). The ΔF in the last generation (i.e., from 1994 to 1999, inclusive) was about 0.20%.

For Meatlinec, 203 ancestors born between 1983 and 1984 (21 males and 182 females) were identified for computation of their long-term contributions to the 2,094 descendants born between 1999 and 2000. The relationship between long-term genetic contributions of these ancestors and their index values is shown in Figure 4a. The regression coefficients of contributions on index scores were not significant for all ancestors (4.1×10^{-5} ; $P = 0.15$), or for ram ancestors (-1.6×10^{-4} ; $P = 0.13$), but were significant for ewes (6.8×10^{-5} ; $P < 0.01$). For the analysis of contributions for the first generation after BLUP evaluation, long-term genetic contributions for the 1,337 ancestors born from 1991 to 1992 (643 males and 694 females) to descendants born between 1999 and 2000 were computed. In this case, the regressions of contributions on index

scores for this set of ancestors were significant for both males (3.6×10^{-5} ; $P < 0.01$) and females (2.4×10^{-5} ; $P < 0.01$).

For Aberdeen Angus, 5,861 ancestors (2,686 males and 3,175 females born between 1976 and 1979) and 48,248 descendants (born between 1995 to 1999) were identified. The regressions of contributions on index score were 3.3×10^{-6} ($P < 0.001$) for all ancestors, 5.7×10^{-6} ($P < 0.001$) for male, and 1.3×10^{-6} ($P < 0.03$) for female ancestors. The analysis of contributions of these male ancestors only having long-term contributions greater than zero gave a regression coefficient (9.3×10^{-5} ; $P = 0.01$) higher than that obtained with all male ancestors. No additional long-term contribution analysis (i.e., for the first generation after BLUP) was carried out due to the long L , which would have implied unconverged contributions.

Expected Increases in Genetic Merit from Applying Optimized Selection

Table 2 shows the optimization results for both populations. Three levels of ΔF constraints (0.5%, 1.0%, and 2.0%) were considered for Meatlinec, and four levels (0.2%, 0.5%, 1.0%, and 2.0%) were considered for Aber-

Table 2. Observed index gain (ΔG_{O-2000}), predicted average index value (Index_{P-2000}), predicted index gain (ΔG_{P-2000}), and number of selected candidates after applying optimized selection with different constraints on the rate of inbreeding (ΔF , %) and predicted index gain under truncation selection (ΔG_{T-2000}) in year 2000 for the Meatlinec and Aberdeen Angus populations^a

Item	ΔF^b			
	0.2	0.5	1.0	2.0
Meatlinec				
ΔG_{O-2000}^c			16.1	
Both sexes optimized				
Index_{P-2000}		285.9	293.5	305.0
ΔG_{P-2000}^d		62.6	70.2	81.7
Selected males		31	26	18
Selected females		49	45	37
Only males optimized				
Index_{P-2000}		230.8	255.5	272.0
ΔG_{P-2000}		7.5	32.2	48.7
Selected males		58	39	19
Selected females		902	902	902
ΔG_{T-2000}^e			27.6	
Aberdeen Angus				
ΔG_{O-2000}	3.6			
Both sexes optimized				
Index_{P-2000}	39.1	40.4	41.9	43.7
ΔG_{P-2000}	21.1	22.4	23.9	25.7
Selected males	68	51	36	17
Selected females	81	58	37	19
Only males optimized				
Index_{P-2000}	33.3	34.3	35.4	36.4
ΔG_{P-2000}	15.2	16.3	17.4	18.4
Selected males	67	41	21	11
Selected females	3,108	3,108	3,108	3,108
ΔG_{T-2000}	11.7			

^aSelection candidates included 395 male and 902 female candidates in Meatlinec and 3,321 male and 3,108 female candidates in Aberdeen Angus.

^bThe observed ΔF in the last generation for Aberdeen Angus and Meatlinec was 0.2 and 1.0%, respectively.

^cThe ΔG_{O-2000} in each population was calculated from the observed average index values in 1999 and 2000: 223.3 and 239.4 index units, respectively, for Meatlinec, and 18.0 and 21.6 index units, respectively, for Aberdeen Angus.

^dThe ΔG_{P-2000} in each population was calculated from the corresponding observed average index value in 1999 and the Index_{P-2000} .

^eThe ΔG_{T-2000} in each population was calculated from the corresponding observed average index values in 1999 and the average index value calculated with equal contributions of males while fixing female contributions equivalent to one mating. The number of males selected was that giving the observed ΔF in each population: 250.9 index units for Meatlinec and 29.7 index units for Aberdeen Angus.

dean Angus. The observed ΔF at the last generation were 1.0% for Meatlinec and 0.2% for Aberdeen Angus.

Optimization of Contributions in Both Sexes. The optimization of contributions of both male and female candidates led to substantial increases in predicted average index score (Index_{P-2000}) and index gain (ΔG_{P-2000}) in 2000 in both populations (Table 2). The observed index gain (ΔG_{O-2000}) from 1999 to 2000 was 16.1 index units for Meatlinec and 3.6 index units for Aberdeen Angus (see Table 2). When ΔF was restricted

to the ΔF observed in the last generation, the ΔG_{P-2000} were 70.2 index units (i.e., 4.4-fold over ΔG_{O-2000}) for Meatlinec ($\Delta F = 1.0\%$) and of 21.1 index units (i.e., around sixfold over ΔG_{O-2000}) for Aberdeen Angus ($\Delta F = 0.2\%$). Further relaxation of the ΔF constraint led to higher increments in index gain. For instance, at the most relaxed constraint ($\Delta F = 2.0\%$), the expected increments over the observed ΔG were 65.6 index units for Meatlinec and 22.1 index units for Aberdeen Angus. However, the relaxation in the restriction on ΔF contributed only to relatively small increases in ΔG in comparison to the increases observed by optimizing contributions. It should be noted that for Meatlinec an increment in ΔG of 46.5 index units was expected even if ΔF was restricted to a value as low as 0.5%, which was the ΔF observed over the post-BLUP period.

At the tightest constraint in ΔF , the number of selected candidates was 80 (i.e., 31 males and 49 females) for Meatlinec and 149 (i.e., 68 males and 81 females) for Aberdeen Angus. As the ΔF restriction was less severe, the number of selected candidates decreased, as expected. For the most relaxed constraint ($\Delta F = 2.0\%$), it dropped down to 55 (i.e., 18 males and 37 females) for Meatlinec and to 36 (i.e., 17 males and 19 females) for Aberdeen Angus.

Optimization of Male Contributions When All Females Are Selected. When a more realistic scenario for typical production systems, where female contributions are restricted, the algorithm still achieved significant predicted increases in index score gains (Table 2). At the observed ΔF in the last generation, ΔG_{P-2000} was 32.2 index units (i.e., twofold over ΔG_{O-2000}) for Meatlinec ($\Delta F = 1.0\%$) and 15.2 index units (i.e., around fourfold over ΔG_{O-2000}) for Aberdeen Angus ($\Delta F = 0.2\%$). As when contributions of both sexes were optimized, the relaxation of the constraint allowed for even higher predicted increases. For the most relaxed constraint ($\Delta F = 2.0\%$), predicted increases in index gain were 32.6 index units for Meatlinec and 14.8 index units for Aberdeen Angus.

For Meatlinec, when ΔF was restricted to a value lower than that observed in the last generation (i.e., 0.5%), ΔG_{P-2000} was 8.6 index units lower than the observed index gain in 2000 as it implied a very tight constraint (Table 2).

Because female contributions were fixed, the expected relative gains over the observed average index scores arose only from the management of the male selection intensity. The number of selected rams in Meatlinec decreased by relaxing the constraint on ΔF from 58 ($\Delta F = 0.5\%$) to 19 ($\Delta F = 2.0\%$), whereas for Aberdeen Angus the number of selected bulls decreased from 67 ($\Delta F = 0.2\%$) to 11 ($\Delta F = 2.0\%$) (Table 2).

The predicted benefits over the observed ΔG might be overestimated because, at the current ΔF , breeders may be able to achieve higher selection intensities if selection were based solely on index values. The rates of gain under truncation selection (i.e., with equal mating proportions) that gave the observed ΔF were 27.6

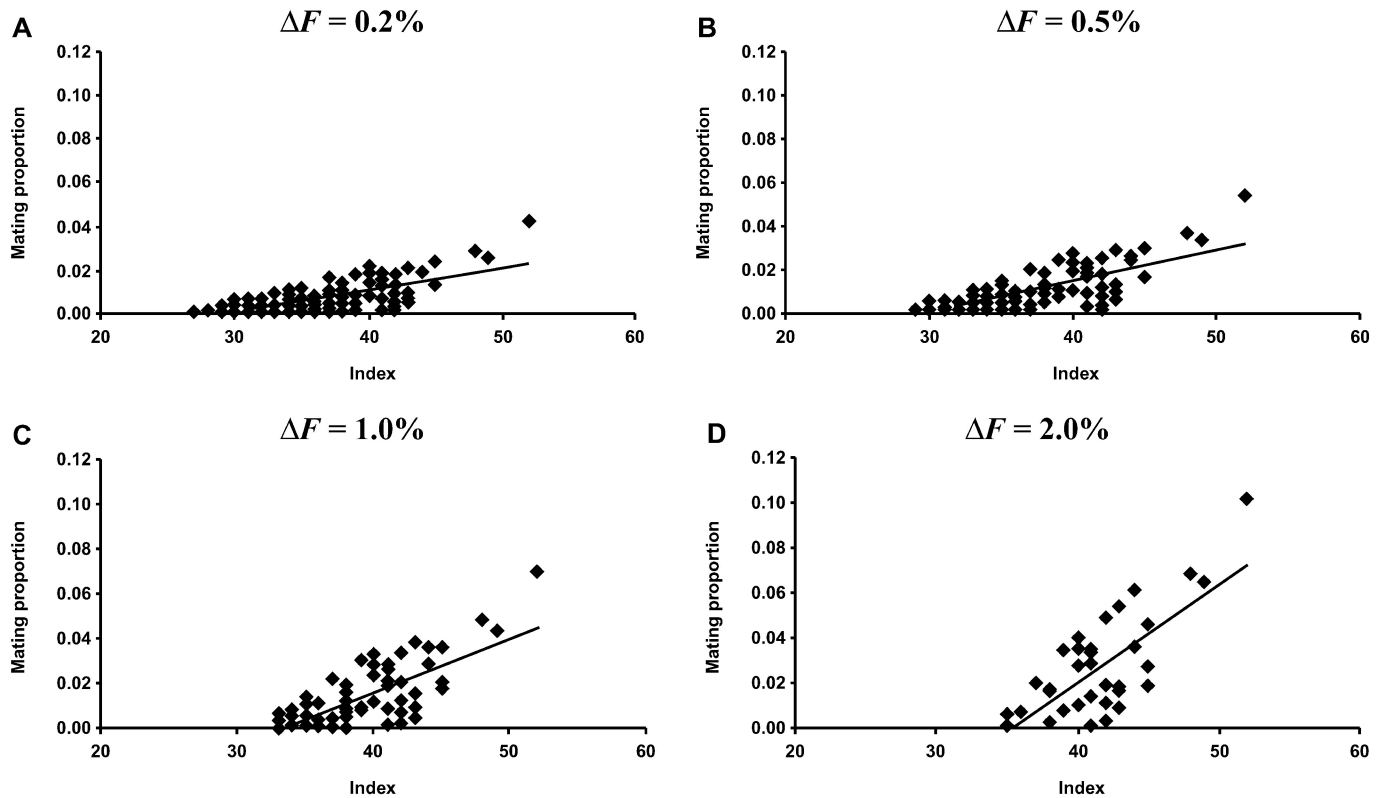


Figure 5. Relationship between optimized mating proportions and index scores of selected candidates for four levels of restriction on the rate of inbreeding (ΔF) when mating proportions of both sexes were optimized for Aberdeen Angus.

index units for Meatline and 11.7 units for Aberdeen Angus (Table 2). Thus, benefits of optimal selection when only male contributions were optimized over truncation selection (based exclusively on EBV) at the observed ΔF were 17% for Meatline and 30% for Aberdeen Angus. This suggests that the above twofold and fourfold expected benefits in ΔG for Meatline and Aberdeen Angus, respectively, may be overpredictions.

Relationship Between Optimized Mating Proportions and Index Scores

To achieve the restriction on ΔF , the more severe the ΔF constraint was, the higher was the number of selected candidates and the more alike were their optimized mating proportions. This behavior across ΔF constraints can be seen in Figure 5 for Aberdeen Angus where selection was mimicked at 1999. The same pattern of behavior was observed for Meatline.

As the ΔF constraint was relaxed, the variance of optimized mating proportions among selected candidates increased from 4.3×10^{-5} ($\Delta F = 0.2\%$) to 4.9×10^{-4} ($\Delta F = 2.0\%$), whereas the variance of the index score among selected candidates decreased from 23.0 ($\Delta F = 0.2\%$) to 13.6 ($\Delta F = 2.0\%$). The highest optimal mating proportion was assigned to the individual with the highest index score (5.20 units) and ranged from 0.042 ($\Delta F = 0.2\%$) to 0.102 ($\Delta F = 2.0\%$).

Discussion

This work has shown that the population structure of the two pedigree breeds analyzed has changed across years and suggests that, in at least one of the populations (i.e., the Meatline), the introduction of BLUP has led to sustained additional genetic gains. Concomitant increases in the average coefficient of inbreeding have been observed, although there was no evidence that ΔF was increased by the introduction of BLUP. The application of dynamic selection tools for maximizing genetic gain while constraining rates of inbreeding to target levels would have led to important benefits in ΔG compared to what has been observed. This demonstrates the scope for this kind of optimization tool in livestock breeding programs.

The Impact of Artificial Insemination

The impact of AI on both populations can be clearly seen in the increase in mating ratios of the breeding males across years. These days, this technique is a standard reproductive technique in beef cattle; however, it is generally less widespread in sheep populations, where the AI procedures are much more complex and success rates are typically much lower. Nevertheless, AI techniques in the United Kingdom have been promoted as one of the key elements for the establish-

ment of sire reference schemes (**SRS**). The SRS enabled BLUP evaluations across flocks and thereby increased the potential benefit from the use of BLUP (Simm, 1998). The widespread use of some sires has not only led to an increase in d , but also in the variance of the number of offspring per male (results not shown).

It might be anticipated that increases in the number of offspring per male and its variance would have led to increases in ΔF . However, ΔF has remained relatively steady, particularly in the Aberdeen Angus. This has been due to the expansion of the recorded breed numbers, and in particular to an increase in the number of bulls used per year in the population over the period studied. This simple step has reduced the proportional contributions of individual males to the gene pool and so limited the expected increase in ΔF .

The Effect of BLUP

The introduction of BLUP evaluations seems to have led to an increase in ΔG for the Meatline, but this response was not observed in the Aberdeen Angus. One reason for this difference is the structure of the populations. Whereas the Meatline consists of four closely cooperating flocks, with selection policies closely defined by the selection index (H. Fell, personal communication), the Aberdeen Angus has a looser breeding pyramid, with about 200 herds and where policies of individual breeders might not be so closely determined by the society alone. Also, in beef cattle, there is likely to be a much higher use of older "proven" males via AI than in sheep. The Meatline may be better placed to utilize the more accurate information arising from the BLUP evaluation, and in combination with AI, the better information across flocks produced by the SRS. A further example of the impact of BLUP in the Meatline is the evidence of increases in L_m during the post-BLUP period where ram usage was extended for a longer period because of the better comparison across age groups made possible by BLUP.

The exclusive use of BLUP-EBV as a ranking tool for truncation selection would be expected to lead to an increase in ΔF (Quinton et al. 1992), due to an increased coselection of relatives. Nevertheless, this phenomenon was not observed in either breed during the post-BLUP period, which may be particularly surprising in the Meatline where closer attention was paid to the index evaluations. However, the increase in breeding males used per year in both populations has proved effective in managing ΔF over the short term. The changes in L_m observed post-BLUP for Meatline would have led to a reduction in ΔF per year, but this benefit would be offset by the larger lifetime genetic contributions arising from rams kept more than 1 yr.

The estimated effective population sizes in the post-BLUP period are 95 for Meatline and 333 for Aberdeen Angus (i.e., ΔF of 0.53 and 0.15% per generation, re-

spectively). These values are above the minimum reference value of 40 animals of Goddard and Smith (1990) for maximizing net genetic response for total economic merit in dairy cattle and fall within the critical range of 30 to 250 animals of Meuwissen and Woolliams (1994) for balancing decreases in fitness due to inbreeding and increases in fitness due to natural selection. Nevertheless, there was a substantial decrease in effective size in Meatline in the last generation to a value comparable to the minimum effective size of 50 recommended by F.A.O. (1998). Thus, the application of methods for avoiding further future increases in ΔF in this population is advisable.

When Meatline ancestors born from 1991 to 1992 were analyzed, those with higher index values tended to have larger long-term contributions because regressions on index values were positive and significant compared to a more uniform relationship between ram usage and index scores during the early establishment phase of this synthetic population. This result clearly coincides with the higher genetic gains achieved after the implementation of BLUP-EBV in 1991. A positive association of contributions with index EBV was also observed in Aberdeen Angus for the only set of ancestors analyzed (i.e., born from 1976 to 1979). For this breed, a comparison of the distribution of contributions before and after the introduction of BLUP is difficult because at most two generations have passed since the introduction. Long-term genetic contributions require five or more generations to achieve a reasonable degree of stability. Higher regressions were observed for male ancestors in both populations, indicating higher selection intensities applied on male than on females in accordance with expectations (Woolliams et al., 1999).

The Effect of Optimized Selection

Although the Meatline has increased its rate of gain using BLUP evaluations and simultaneously managed its ΔF by increasing the number of males selected per year (so reducing the selection intensity), further gains are possible by using the selection algorithms. The results showed that these algorithms would benefit both Aberdeen Angus and Meatline over a range of values of ΔF . The most dramatic increases in ΔG were obtained when selection was allowed in both males and females. However, these gains assume unrealistic reproductive rates for females. Substantial and valuable increases in ΔG were obtained when no selection among females was allowed. At the ΔF in the last generation, the benefits over the observed ΔG were 16.1 index units (i.e., twofold) for Meatline and 11.6 index units (i.e., threefold) for Aberdeen Angus.

The comparisons of the expected (from optimized mating proportions) with observed index scores, implicitly assumed that in practice selection in the two populations has been exclusively based on index values. In practical breeding schemes, however, selection decisions are based not only on EBV, but also on other

factors (e.g., physical and reproductive soundness). This reduces the selection intensity and the maximum genetic merit achievable. For instance, Lewis and Simm (2000) found that losses in selection intensity in sheep SRS lead to genetic response 0.58 to 0.69 times that obtained when strictly the best animals were selected on BLUP-EBV. Results in Meatline support this expectation, where the ratio $\Delta G_{O-2000}/\Delta G_{T-2000}$ was 0.58 (see Table 2). This effect was more important in Aberdeen Angus, where the ratio $\Delta G_{O-2000}/\Delta G_{T-2000}$ was only 0.31. In this case, because of the scale of population, selection decisions might be restricted within herds or groups of breeders. In contrast, the Meatline SRS is managed as a single selection unit with a single selection policy and tight cooperation among flocks (H. Fell, personal communication). The predicted benefits of 17% for Meatline and 30% for Aberdeen Angus over the expected gain under truncation selection provides an even more realistic evaluation of the benefits of optimal selection when compared to traditional truncation selection based solely on BLUP-EBV. In addition, deterministic predictions of the rate of genetic gain at predefined rates of inbreeding (our unpublished observations) showed expected increases ranging from 20 to 40% for $\Delta F = 1.0\%$.

The ΔG from optimal selection after optimizing only male contributions of 15.2 index units (see Table 2) at the observed ΔF in Aberdeen Angus was similar to the expected ΔG (i.e., 15.7 index units, result not shown) after optimizing the contributions of selected bulls in 1999 with observed offspring in 2000 conditional to the observed dam contribution. This indicates that the expected extra index gain from optimal selection are realistic and would be achievable by only optimizing the usage of the current set of bulls selected by the breeders using the available selection index.

In practice, about 30 rams and 700 ewes are used each year in Meatline, but when contributions of both sexes were optimized, the optimization algorithm implied selection of 25 males and 43 females on average (Table 2). Similarly, in Aberdeen Angus the actual numbers of breeding animals (about 1,000 males and 10,000 females) are much larger than those obtained after applying the optimization tool on both sexes (43 males and 49 females on average, Table 2). As pointed out before, these optimum numbers of selected candidates imply very high reproductive rates, particularly on the female side. On the other hand, much more realistic outcomes from the application of the optimization tool were obtained when only male contributions were optimized conditional to fixed female contributions. At the observed ΔF , the maximum contribution allocated to a male was about 0.046 and 0.048 for Meatline and Aberdeen Angus, respectively. This is equivalent to an expected maximum optimum number of matings per male of 83 (i.e., $2 \times 0.046 \times 902$) for Meatline and 298 (i.e., $2 \times 0.048 \times 3,108$) for Aberdeen Angus. These optimum numbers and the differential usage arising from optimizing contributions can be

readily achieved through AI, which is currently a standard male reproductive technique. Moreover, they imply a maximum number of offspring per male that are well below the observed upper limit for the number of offspring per male range in each breed (see Table 1).

The change in the slope and intercept of the regression coefficient between mating proportions and index scores with different restrictions on ΔF observed here agrees with the general form of the optimal solutions stated by Grundy et al. (1998). Basically, as a less severe constraint was imposed, fewer individuals were selected, the usage of the individuals became more unequal, and the slope of the regression was higher (Figure 5). Although in the initial cohorts after applying the dynamic selection tools the selective advantage may be the index EBV as suggested by Figure 5, once the use of the dynamic selection algorithm is established, the selection advantage is given by the estimated Mendelian sampling term of the index (Woolliams et al., 2002).

Weigel and Lin (2002) applied the algorithm of Meuwissen (1997) in five major U.S. dairy breeds, concluding that genetic gain may be sacrificed by imposing constraints on inbreeding. Their conclusion could be somewhat misleading because they did not compare the predicted average genetic merit from the optimization to that obtained without optimization at the observed level of inbreeding. Our results clearly indicate that no losses of gain are expected when the inbreeding rate is constrained to the observed value, but additional gains are expected. The only situation where a lower relative gain with respect to the observed gain was obtained, occurred in the extreme case when a constraint equivalent to a lower than the observed ΔF in Meatline was applied, after fixing all female contributions.

The practical realization of the optimal contributions and the average expected index scores requires a coordinated policy of the use of selected candidates among the different breeding flocks or herds making up the breeding population. This could be a reasonable target in small-scale schemes with coordinated breeding policies, but clearly would be much more difficult in large schemes in which different objectives might be pursued. Hence, in breeds with large-scale breeding programs, a more reasonable approach would be to apply the optimization tool on individual herds or groups of herds with coordinated selection policies and objectives.

Two methodological aspects of this optimization should be addressed. Firstly, the use of EBV obtained in 2000 to mimic selection in 1999, instead of using the EBV obtained in 1999, is not expected to have affected the results obtained because no significant changes in candidate ranking were found when EBV from both evaluations were compared. Secondly, the preselection of candidates would not have affected the optimization outcome. Among the group of higher merit candidates, those in the bottom half were never

selected, indicating that any discarded candidate would not have made a significant contribution if it had been included in the optimization. On the other hand, this allowed a significant reduction of computational requirements.

More flexible constraints may be required in breeding programs with particular features or breeding structure. These may include setting a maximum contribution per male (i.e., a minimum number of sires), a fixed contribution for a particular set of males, or a desired contribution of a group of females (e.g., in a nucleus). These constraints can be accommodated with the same tool used here (after Appendix in Meuwissen, 1997). For instance, for Meatline, an additional optimization with a maximum number of 20 female mates per selected ram (i.e., a minimum of 45 selected rams) was set (not shown). Accordingly, the selection tool found a feasible solution by selecting 46 males, of which 45 were allocated a maximum fixed contribution of 0.01. Moreover, even with this highly restrictive constraint, the expected ΔG at the current ΔF was still about 6.0 index units higher than the observed ΔG .

Although the optimization approach used here can be realistically applied in practical livestock breeding programs, evolutionary computation strategies may provide a more flexible framework for setting a greater variety of constraints. Genetic algorithms have been used as optimization tools in livestock breeding programs (e.g., Shepherd and Kinghorn, 1998, Meszaros et al., 1999), and they could be extended to explicitly restrict ΔF (e.g., Correnti, 2002).

After allocating optimal mating proportions to the selected candidates, the following step in a breeding program is to decide a mating policy. Sonesson and Meuwissen (2000) found that the optimization tool used here combined with mating systems that restricted either mating pairs coancestry or offspring coancestry, achieved 22% higher response than random mating, in particular for stringent constraints on ΔF . Nevertheless, the extra benefit from the use of nonrandom matings was reduced as the size of the scheme increased.

Our results refer to practical livestock populations in which the main objective is to achieve the highest genetic gain for a given ΔF . However, the approach is also valid for conservation purposes in which the aim may be to minimize ΔF while achieving a predefined level of genetic gain (Villanueva et al., 2003). Hence, genetic improvement and conservation can be taken as the extremes of a broader optimization problem with particular relative emphasis given to the gain and inbreeding.

Implications

This work demonstrates that the application of dynamic optimization tools allows the management of the rate of inbreeding without any concomitant loss in genetic gain. At the observed rate of inbreeding,

substantial benefits were predicted over the expected genetic gains under truncation selection based exclusively on index values and indeed over the observed gains in these two distinct populations of sheep and beef cattle. Breeders have now the opportunity of explicitly managing the risk associated with inbreeding and to adopt breeding policies according with their risk preferences. The only inputs needed to apply the tool are the estimated breeding values, currently available from genetic evaluations, and an estimate of inbreeding level in the population. The realization of the benefits from the application of dynamic selection tools requires a coordinated policy on the use of selected candidates among the different breeding flocks or herds making up the breeding population.

Literature Cited

- Amer, P., R. Crump, and G. Simm. 1998. A terminal sire selection index for U.K. beef cattle. *Anim. Sci.* 67:445–454.
- Bijma, P., and J. A. Woolliams. 1999. Prediction of genetic contributions and generation intervals in populations with overlapping generations under selection. *Genetics* 151:1197–1210.
- Burrow, H. M. 1993. The effects of inbreeding in beef cattle. *Anim. Breed. Abstr.* 61:737–751.
- Correnti, G. 2002. Optimisation with constraints in animal breeding. M.S. thesis, School of Computing, Napier Univ., Edinburgh, U.K.
- F.A.O. 1998. Management of small populations at risk. Secondary guidelines for the development of national farm genetic resources management plans. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Goddard, M. G., and C. Smith. 1990. Optimum number of bull sires in dairy cattle breeding. *J. Dairy Sci.* 73:1113–1122.
- Grundy, B., B. Villanueva, and J. A. Woolliams. 1998. Dynamic selection procedures for constrained inbreeding and their consequences for pedigree development. *Genet. Res.* 72:159–168.
- Grundy, B., B. Villanueva, and J. A. Woolliams. 2000. Dynamic selection for maximizing response with constrained inbreeding in schemes with overlapping generations. *Anim. Sci.* 70:373–382.
- Lamberson, W. R., and D. L. Thomas. 1984. Effects of inbreeding in sheep: A review. *Anim. Breed. Abstr.* 52:287–297.
- Lewis, R. M., and G. Simm. 2000. Selection strategies in sire referencing schemes in sheep. *Livest. Prod. Sci.* 67:129–141.
- Meuwissen, T. H. E. 1997. Maximizing the response of selection with predefined rate of inbreeding. *J. Anim. Sci.* 75:934–940.
- Meuwissen, T. H. E., and Z. Luo. 1992. Computing inbreeding coefficient in large populations. *Genet. Sel. Evol.* 24:305–313.
- Meuwissen, T. H. E., and J. A. Woolliams. 1994. Effective sizes of populations to prevent a decline in fitness. *Theor. Appl. Genet.* 89:1019–1026.
- Meuwissen, T. H. E., and A. K. Sonesson. 1998. Maximizing the response of selection with predefined rate of inbreeding: Overlapping generations. *J. Anim. Sci.* 76:2575–2583.
- Meszaros, S. A., R. G. Banks, J. H. J. van der Werf, and M. E. Goddard. 1999. The use of genetic algorithms for optimizing age structure in breeding populations when inbreeding depresses genetic gain through effects on reproduction. *Anim. Sci.* 68:449–457.
- M.L.C. 1999. Sheep yearbook. Meat and Livestock Commission, Milton Keynes, U.K.
- Quinton, M., C. Smith, and M. E. Goddard. 1992. Comparison of selection methods at the same level of inbreeding. *J. Anim. Sci.* 70:1060–1067.
- Shepherd, R. K., and B. P. Kinghorn. 1998. A tactical approach to the design of crossbreeding programs. *Proc. 6th World Cong Genet. Appl. Livest. Prod. Armidale, Australia.* 25:431–438.

- Simm, G. 1998. Genetic improvement of cattle and sheep. Farming Press, Ipswich, U.K.
- Simm, G., and W. S. Dingwall. 1989. Selection indices for lean meat production in sheep. *Livest. Prod. Sci.* 21: 223–233.
- Sonesson, A. K. and T. H. E. Meuwissen. 2000. Mating schemes for optimum contribution selection with constrained rates of inbreeding. *Genet. Sel. Evol.* 32: 231–248.
- Villanueva, B., R. Pong-Wong, J. A. W. Woolliams, and S. Avendaño. 2003. Managing genetic resources in selected and conserved populations. In *Farm Animal Genetic Resources*. G. Simm, B. Villanueva, K. D. Sinclair, and S. Townsend, ed. BSAS Occasional Publication No. 30. Nottingham Univ. Press, Nottingham, U.K. (In press).
- Weigel, K. A., and S. W. Lin. 2002. Controlling inbreeding by constraining the average relationship between parents of young bulls entering AI progeny test programs. *J. Dairy Sci.* 85:2376–2383.
- Woolliams, J. A., and E. A. Mäntysaari. 1995. Genetic contributions of Finnish Ayrshire bulls over four generations. *Anim. Sci.* 61:177–187.
- Woolliams, J. A., P. Bijma, and B. Villanueva. 1999. Expected genetic contributions and their impact on gene flow and genetic gain. *Genetics* 153:1009–1020.
- Woolliams, J. A., R. Pong-Wong, and B. Villanueva. 2002. Strategic optimization of short- and long-term gain and inbreeding in MAS and non-MAS schemes. Communication No.32-02 on CD-ROM. Proc. 7th World Cong. Genet. Appl. Livest. Prod., Montpellier, France.
- Wray, N., and R. Thompson. 1990. Prediction of rates of inbreeding in selected populations. *Genet. Res.* 72:41–54.

References

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