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GROUP RECORDS WITH GENOMIC PREDICTON CONVERT ACCURACY INTO GENETIC GAIN MORE EFFICIENTLY THAN PEDIGREE PREDICTION

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SUMMARY

We tested the premise that genomic prediction (GBLUP) converts accuracy into genetic gain (ΔG) more efficiently than pedigree prediction (PBLUP) using group records at the same rate of true inbreeding (ΔF). We tested this premise by stochastic simulation. We estimated conversion efficiency (CE) of optimum-contribution selection (OCS) using individual and group records with PBLUP and GBLUP at 0.01 ΔF. We did this by allocating selection candidates to groups of 12 individuals. Animals in each group were measured as either individual or group records. Selection was for a single trait with heritability 0.2. The trait was controlled by 7702 biallelic quantitative-trait loci. We found that the CE of group records increased from 94 to 102% when we changed prediction from PBLUP to GBLUP. Group records generated EBV that were about 0.76 times as accurate as individual records with both PBLUP and GBLUP. However, group records realised only 0.70 times as much ΔG as individual records with PBLUP; they realised 0.79 times as much ΔG with GBLUP. Clearly, group records converted accuracy into ΔG more efficiently with GBLUP than they did with PBLUP. This makes group records a more attractive measure of phenotypic performance with GBLUP.

INTRODUCTION

Group records measure the sum of phenotypic performances of animals reared in groups (e.g., feed intake of pigs in a pen). They can be particularly useful for traits that are difficult or expensive to measure as individual records (i.e., phenotypic performance of individual animals). Not only are group records often easier and cheaper to measure than individual records, estimated breeding values (EBV) predicted using group records are typically 50-90% as accurate as EBV using individual records (Olson *et al.* 2006, Su *et al.* 2018, Ma *et al.* 2020). This prompted a widely-held view that selection based on group records could realise most of the genetic gain (ΔG) realised by individual records at a fraction of the cost. However, Henryon *et al.* (*in prep.*) found that group records were only 82-90% as efficient in converting accuracy into ΔG as individual records – a parameter they referred to as conversion efficiency (CE). In their study, selection candidates were grouped and phenotyped, breeding values (BV) were predicted as BLUP of breeding values based on pedigree information (PBLUP), and selection was carried out by optimum-contribution selection (OCS) with rate of pedigree inbreeding constrained to 0.01. They found that group records had lower CE than individual records because OCS using group records reduced selection intensities. Selection intensities were reduced because EBV with group records expressed less within-family variation and candidates that ranked highest for EBV were more related. To realise the constrained rate of pedigree inbreeding, OCS using group records needed to select more candidates than OCS using individual records. This implies that if group records are to generate higher CE, we need EBV with more within-family variation. One way to do this is to replace PBLUP with genomic prediction of BV (GBLUP). With GBLUP, group records should generate higher selection intensities by enabling OCS to differentiate between candidates within full-sib families. Fewer candidates would need to be selected to realise the same rate of inbreeding as OCS using group records with PBLUP. This

reasoning led us to believe that GBLUP results in higher CE than PBLUP when using group records at the same rate of inbreeding. We tested this premise by stochastic simulation.

MATERIALS AND METHODS

Procedure. We used stochastic simulation of animal-breeding schemes to estimate CE generated by OCS using individual and group records with PBLUP and GBLUP at 0.01 rate of true inbreeding (ΔF), where the true inbreeding coefficient of an individual was defined as the observed proportion of loci in its genome with alleles that are identical-by-descent (IBD). We allocated selection candidates to groups of 12 individuals. Animals in each group were measured as either individual or group records. We also sampled relatives of the selection candidates. These animals were measured as individual records. They were included in the prediction models, but were not candidates for selection. Selection was for a single trait with heritability 0.2 (additive-genetic variance 1.0). The trait was controlled by 7702 biallelic quantitative-trait loci (QTL). It was also influenced by litter and group effects (litter and group variances 0.25). All animals were genotyped and phenotyped before selection in each generation. Breeding schemes were run for eight discrete generations (t = 1 … 8) and replicated 120 times. Each replicate was initiated by sampling a unique base population from a founder population. Animals in the base populations were randomly selected in generation t = 1. In generations t = 2 … 8, selection candidates were allocated matings by OCS.

Breeding scheme. A total of 600 matings were allocated to 3600 selection candidates by OCS in generations t = 2 … 10. The number of matings that were allocated to each male could vary from 0, 1, 2 … to 50 matings. Six-hundred females were allocated a single mating. The matings allocated to the sires and dams were paired randomly. Each dam produced seven offspring – four males and three females – resulting in 600 full-sib families and 4200 offspring (2400 males and 1800 females). Three males and three females from each full-sib family were randomly pre-selected as candidates for selection. These 3600 animals were allocated to groups of 12 and measured as individual or group records. The remaining male in each full-sib family was measured as an individual record but was not a candidate for selection. The BV of the selection candidates were predicted using their own phenotypes and their genetic relationships to the male in each full-sib family that was measured as an individual record.

Grouping criterion. Groups of 12 animals were established by dividing each full-sib family into two sub-families of three full-sibs. Four sub-families from four different full-sib families were randomly allocated to each group. Each full-sib family was represented in two groups. Selection candidates were allocated to a total of 300 groups in each generation.

Genetic model. The founder population was established using a Fisher-Wright inheritance model to generate linkage disequilibrium between QTL and markers. The genome was 30 M and consisted of 18 pairs of autosomal chromosomes. Each chromosome was 167 cM long. The genome contained 7702 QTL and 54218 biallelic markers. These markers were randomly distributed across the genome and in linkage disequilibrium with the QTL. They were used in GBLUP. An additional 6012 IBD loci were placed evenly across the genomes of animals in base populations. Unique alleles at these loci were used to calculate ΔF.

Optimum-contribution selection. OCS was carried out by maximising $\mathbf{U}_t(\mathbf{c}) = \mathbf{c}'\hat{\mathbf{a}} - \omega\mathbf{c}'\mathbf{A}\mathbf{c}$, where $\mathbf{c}$ is a vector of genetic contributions to the next generation, $\hat{\mathbf{a}}$ is a vector of BV predicted with PBLUP or GBLUP, ω is a penalty applied to the average-estimated relationship of the next generation, and $\mathbf{A}$ is a pedigree-relationship matrix (after Henryon *et al.* 2019). The penalty, ω, was constant across generations. It was calibrated to realise 0.01 ΔF. The realisedΔF deviated from 0.01 by less than 0.0001.

Statistical analyses. We present CE, accuracy, ΔG, selection intensity, and additive-genetic standard deviation realised by OCS using individual and group records with PBLUP and GBLUP. CE measured the efficiency by which accuracy of EBV from group records was converted to ΔG

relative to individual records: $\mathrm{CE} = \frac{\Delta \mathrm{G}_j / \Delta \mathrm{G}_{ind}}{r_j / r_{ind}} \cdot 100$, where $\Delta \mathrm{G}_j$ and r_j are mean ΔG and accuracy of individual or group records (*j* = *ind*, *grp*). ΔG, accuracy, selection intensity, and additive-genetic standard deviation are presented as means (± sd) of the 120 replicates. ΔG in each replicate was calculated as the linear regression of G_t on *t*, where G_t is the average true breeding value of animals born at times $t = 4 \ldots 8$. Accuracy, selection intensity, and additive-genetic standard deviation in each replicate were averaged over generations $t = 4 \ldots 8$. Accuracy was calculated as the correlation between true breeding values and EBV of animals within generation. Selection intensity was calculated as the difference in average EBV of selected animals weighted by their contribution to the next generation and average EBV of selection candidates within generations divided by the standard deviation of the EBV. Additive-genetic standard deviation was calculated as the standard deviation of true breeding values of animals within generations. We present absolute and scaled ΔG, accuracy, selection intensity, and additive-genetic standard deviation. Scaling was carried out by setting values realised by individual records with PBLUP and GBLUP to 100. ΔF in each replicate was calculated as 1-exp(β), where β is the linear-regression coefficient of $\ln(1\text{-}F_t)$ on *t,* and F_t is the average coefficient of true inbreeding for animals born at times $t = 4 \ldots 8$ (after Sonesson *et al.* 2004).

RESULTS AND DISCUSSION

Our findings supported our premise that GBLUP results in higher CE than PBLUP when using group records at the same rate of inbreeding. We found that the CE of group records increased by eight percentage units – from 94 to 102% – when we changed prediction from PBLUP to GBLUP at 0.01 ΔF (Table 1). When prediction was changed from PBLUP to GBLUP, the accuracy of both individual and group records increased by about 1.4 times. That is, the relative difference in accuracy between individual and group records remained the same: group records generated EBV that were about 0.76 times as accurate as individual records with both PBLUP and GBLUP. However, group records realised only 0.70 times as much ΔG as individual records with PBLUP. They realised 0.79 times as much ΔG with GBLUP. Clearly, group records converted accuracy into ΔG more efficiently with GBLUP than they did with PBLUP. It suggests that the widely-held view that selection based on group records could realise most of the ΔG realised by individual records at a fraction of the cost is more applicable to GBLUP than it is to PBLUP. Of course, the ultimate decision of whether to invest in individual or groups records to measure difficult and expensive traits will be specific for each breeding scheme. It will depend on the relative cost and difficulty of gathering individual and group records and how managers of breeding schemes evaluate returns of investment. So, groups records are a more attractive measure of phenotypic performance with GBLUP than with PBLUP because they convert accuracy into ΔG more efficiently.

As we contented, OCS using group records generated higher CE with GBLUP than they did with PBLUP because selection intensity of OCS using group records relative to individual records was higher with GBLUP. We found that selection intensity using group records was only 0.89 times as high as individual records with PBLUP (Table 1). It was 0.95 times as high with GBLUP. The selection intensity of OCS using group records was higher with GBLUP presumably because genomic relationships generated more within-family variation for EBV. OCS using group records with GBLUP was able to differentiate between candidates within full-sib families. It could select fewer candidates to realise 0.01 ΔF than group records with PBLUP. Therefore, group records generate higher CE with GBLUP than PBLUP because they increase selection intensities by generating more within-family variation for EBV.

Table 1. Conversion efficiency, accuracy, rate of genetic gain, selection intensity, and additive-genetic standard deviation realised by individual and group records at 0.01 ΔF with two predictions methods (PBLUP and GBLUP)

Prediction	Record	CE	r	ΔG	i	σ_a	r*	ΔG*	i^*	σ_a^*
PBLUP	Individual	100	0.54	0.73	1.70	0.83	100.0	100.0	100.0	100.0
	Group	94	0.40	0.51	1.50	0.88	74.4	70.3	88.7	107.0
GBLUP	Individual	100	0.74	1.01	1.83	0.75	100.0	100.0	100.0	100.0
	Group	102	0.57	0.80	1.74	0.82	77.3	79.1	95.3	109.5

Absolute and scaled accuracies (r and r*), rates of genetic gain (ΔG and ΔG*), selection intensities (i and i^*), and additive-genetic standard deviation (σ_a and σ_a^*) are means of 120 simulation replicates. r*, ΔG*, i^*, and σ_a^* were calculated by setting r, ΔG, i, and σ_a realised by individual records to 100 with PBLUP and GBLUP. SD between replicates ranged from 0.012 to 0.035 (r), 0.040 to 0.057 (ΔG), 0.030 to 0.091 (i), 0.144 to 0.180 (σ_a), 1.58 to 6.49 (r*), 3.99 to 7.81 (ΔG*), 1.66 to 4.96 (i^*), and 19.21 to 24.00 (σ_a^*).

We were surprised to find that CE was greater than 100 for group records with GBLUP. It was greater than 100 because there was more additive-genetic variation available for OCS using group records to convert accuracy into ΔG than OCS using individual records. Unlike selection intensity, the relative difference in additive-genetic variation between individual and group records remained the same with PBLUP and GBLUP: the additive-genetic standard deviation of OCS using group records was about 1.08 times higher than OCS using individual records (Table 1). More additive-genetic variation was available for OCS using groups records because selection was not as effective as individual records. It realised less ΔG, leading to less Bulmer effect and smaller changes in allele frequencies. So, CE of group records using GBLUP can be higher than 100 because OCS using group records results in more additive-genetic variation available to be converted into ΔG.

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