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Including nonadditive genetic effects in mating programs to maximize dairy farm profitability

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ABSTRACT

We compared the outcome of mating programs based on different evaluation models that included nonadditive genetic effects (dominance and heterozygosity) in addition to additive effects. The additive and dominance marker effects and the values of regression on average heterozygosity were estimated using 632,003 single nucleotide polymorphisms from 7,902 and 7,510 Holstein cows with calving interval and production (milk, fat, and protein yields) records, respectively. Expected progeny values were computed based on the estimated genetic effects and genotype probabilities of hypothetical progeny from matings between the available genotyped cows and the top 50 young genomic bulls. An index combining the traits based on their economic values was developed and used to evaluate the performance of different mating scenarios in terms of dollar profit. We observed that mating programs with nonadditive genetic effects performed better than a model with only additive effects. Mating programs with dominance and heterozygosity effects increased milk, fat, and protein yields by up to 38, 1.57, and 1.21 kg, respectively. The inclusion of dominance and heterozygosity effects decreased calving interval by up to 0.70 d compared with random mating. The average reduction in progeny inbreeding by the inclusion of nonadditive genetic effects in matings compared with random mating was between 0.25 to 1.57 and 0.64 to 1.57 percentage points for calving interval and production traits, respectively. The reduction in inbreeding was accompanied by an average of A\$8.42 (Australian

dollars) more profit per mating for a model with additive, dominance, and heterozygosity effects compared with random mating. Mate allocations that benefit from nonadditive genetic effects can improve progeny performance only in the generation where it is being implemented, and the gain from specific combining abilities cannot be accumulated over generations. Continuous updating of genomic predictions and mate allocation programs are required to benefit from nonadditive genetic effects in the long term.

Key words: planned mating, nonadditive genetic effect, inbreeding, specific combining ability

INTRODUCTION

Mate selection, the simultaneous selection of animals and allocating mates, is an important component of every breeding program to guarantee the optimal contribution of parents to future generations (Kinghorn, 2011). The main reasons to implement mate selection in livestock are to optimize progeny performance and control inbreeding. It can also be used to increase the connectedness between herds, inform culling decisions, exploit the benefit of nonadditive genetic effects, and manage the genotypic frequencies of specific markers (e.g., targeting genetic defects, as in Cole, 2015).

In dairy cattle breeding, mate selection programs may be particularly important, as the strong directional selection to improve productive traits has caused a reduction in effective population size and, therefore, an increase in inbreeding. This leads to reduced population fitness (i.e., fertility and survival) by increasing the frequency of recessive deleterious alleles (Smith et al. 1998; Weigel and Lin, 2000; Weigel, 2001).

Mating programs in dairy cattle and other livestock have traditionally controlled rates of inbreeding by using pedigree information to avoid matings between animals with a common ancestor. Inbreeding coeffi-

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cients calculated from pedigree data have been used to exclude matings that may give rise to conditions controlled by lethal mutations in addition to those that negatively affect phenotypic means and genetic variances and consequently limit genetic progress within populations. Optimal genetic contribution (Wray and Goddard, 1994; Meuwissen, 1997) is an example of a selection strategy that aims to maximize the selection differential at a constrained rate of inbreeding in the future breeding population using pedigree information.

Inbreeding can also be calculated using genomic information (VanRaden, 2007, 2008). The availability of high-density SNP panels on large numbers of animals has transformed the structure of dairy breeding, where genomic breeding values are now being used to select elite sires and dams entering to national breeding programs (Haves et al., 2009; Hutchison et al., 2014). This has led to more rapid genetic progress by shortening the generation interval compared with conventional progeny testing; however, this has come at the cost of accumulation of more inbreeding per unit of time through increasing the number of generations per unit of time (Pryce and Daetwyler, 2012). Nonetheless, it has been argued that when the selection of animals is based on genomic information, genomic measures of inbreeding are better at controlling inbreeding than pedigree information (Pryce et al., 2012), and this may be more effective across generations (Sonesson et al., 2012). Furthermore, inbreeding coefficients calculated from SNP do not require pedigree data, which avoids the biases from errors in pedigree recording and lack of depth of pedigrees (Pryce et al., 2012). Another advantage of genomic measures of inbreeding is that they reflect the actual proportion of the genome shared by individuals and are more accurate than pedigree-based measures, which are only the expected fractions of the genome identical by descent. This has been demonstrated by Keller et al. (2011), who found higher correlations in human data between genomic measures of inbreeding and homozygous mutation load, the driver of inbreeding depression, than using pedigree-based inbreeding coefficients and concluded that genomic estimates of inbreeding are better indicators of inbreeding depression.

Genomic information also offers new possibilities to estimate nonadditive genetic effects (i.e., dominance and epistasis) of markers. Genetic evaluations typically predict additive values of alleles and ignore nonadditive genetic effects because it is the additive genetic merit of individuals that is transmitted directly across generations. However, the total genetic value of an animal is a function of both additive and nonadditive effects, and these effects together could be better predictors of future phenotypes (e.g., Aliloo et al., 2016; Lopes et al., 2016). The estimation of epistatic effects suffers from the large increase in dimensionality, but dominance effects can be estimated simultaneously with additive genetic effects and summed across loci (Toro and Varona, 2010; Vitezica et al., 2013). For mating programs, the information on genotypes can also be used to calculate genotype probabilities of hypothetical progeny resulting from possible matings between candidates (Toro and Varona, 2010; Sun et al., 2013). These probabilities together with the estimated additive and dominance effects of marker genotypes can be used to generate the total genetic merit of individuals, which can then be used for mate allocation. Ertl et al. (2014) compared 2 different mating scenarios for milk and protein yields of Fleckvieh cows where, in the first, selection of the mates was based on only additive genetic effects whereas the other also included dominance effects for mate selection. They found that mate selection based on total genetic values (additive plus dominance) would provide a larger expected total genetic superiority in progeny (i.e., 14.8 and 27.8% for milk and protein yields, respectively), but would reduce the expected additive genetic gain by only 4.5% for milk yield and 2.6% for protein yield. In a simulation study by Toro and Varona (2010), the advantage of including dominance effects in addition to additive effects in the evaluation model was 9 to 14% at different values of additive and dominance heritabilities for random mating; using mate allocation provided an additional response ranging from 6 to 22%. It should be noted that, in contrast to heritable additive genetic effects, the extra gain from dominance gene actions cannot be accumulated over generations because it depends on the interaction between the inherited maternal and paternal gametes in each generation.

The aims of our study were to compare mating programs with and without nonadditive genetic effects (dominance and heterosis) for optimizing productivity and functionality of progeny performance (i.e., maximize milk, fat, and protein yields and minimize calving interval), and to investigate their effect on inbreeding in the next generation in a large dairy cattle data set. The genotypic values of SNP markers were estimated using real cow data and then summed across loci based on genotype probabilities of hypothetical progeny to calculate the expected progeny values.

MATERIALS AND METHODS

Data

In total, 7,902 Holstein cows were genotyped with the Bovine SNP50 Illumina array (Illumina, San Diego, CA). Their 50K genotypes were imputed to high-

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