



How genomic selection has increased rates of genetic gain and inbreeding in the Australian national herd, genomic information nucleus, and bulls

B. A. Scott,^{1,2} M. Haile-Mariam,^{2*} B. G. Cocks,^{1,2} and J. E. Pryce^{1,2}

¹Agriculture Victoria Research, AgriBio, Centre for AgriBioscience, Bundoora, Victoria 3083, Australia

²School of Applied Systems Biology, La Trobe University, Bundoora, Victoria 3083, Australia

ABSTRACT

Genomic selection has been commonly used for selection for over a decade. In this time, the rate of genetic gain has more than doubled in some countries, while inbreeding per year has also increased. Inbreeding can result in a loss of genetic diversity, decreased long-term response to selection, reduced animal performance and ultimately, decreased farm profitability. We quantified and compared changes in genetic gain and diversity resulting from genomic selection in Australian Holstein and Jersey cattle populations. To increase the accuracy of genomic selection, Australia has had a female genomic reference population since 2013, specifically designed to be representative of commercial populations and thus including both Holstein and Jersey cows. Herds that kept excellent health and fertility data were invited to join this population and most their animals were genotyped. In both breeds, the rate of genetic gain and inbreeding was greatest in bulls, and then the female genomic reference population, and finally the wider national herd. When comparing pre- and postgenomic selection, the rates of genetic gain for the national economic index has increased by ~160% in Holstein females and ~100% in Jersey females. This has been accompanied by doubling of the rates of inbreeding in female populations, and the rate of inbreeding has increased several fold in Holstein bulls since the widespread use of genomic selection. Where cow genotype data were available to perform a more accurate genomic analysis, greater rates of pedigree and genomic inbreeding were observed, indicating actual inbreeding levels could be underestimated in the national population due to gaps in pedigrees. Based on current rates of genetic gain, the female reference population is pro-

gressing ahead of the national herd and could be used to infer and track the future inbreeding and genetic trends of the national herds.

Key words: genetic gain, genomic selection, inbreeding, reference populations

INTRODUCTION

Over the last decade, genetic improvement in countries with advanced dairy industries has been based on genomic selection (GS). Genetic selection uses marker genotypes and phenotypes in a reference population (RP) to predict breeding values of selection candidates that have been genotyped (Meuwissen et al., 2001). The rate of genetic gain and inbreeding under GS in dairy cows has not been assessed in Australia. However, GS has doubled the rate of genetic gain in dairy cattle populations in various countries (e.g., United States, García-Ruiz et al., 2016; and France, Doublet et al., 2019). This has been primarily driven by the ability to predict an animal's performance at a younger age with increased accuracy, resulting in the reduction of the generation interval and increase in selection intensity (García-Ruiz et al., 2016).

Although GS was initially expected to reduce the rate of inbreeding per generation (de Roos et al., 2011), recent studies in Dutch, French and North American Holsteins indicate the contrary, where increases in the rate of inbreeding per year have been observed (Doekes et al., 2018; Forutan et al., 2018; Doublet et al., 2019). Inbreeding results in increased homozygosity at the genomic level and has been shown to increase the prevalence of undesirable genetic disorders (e.g., complex vertebral malformation; Schütz et al., 2008), loss of genetic diversity (e.g., Goddard, 2009), and inbreeding depression (Pryce et al., 2014). Inbreeding depression negatively affects fitness and milk production traits (González-Recio et al., 2007; McParland et al., 2007; Bjelland et al., 2013).

Different strategies to manage inbreeding have been proposed, such as optimal contribution selection (Meuwissen, 1997; Grundy et al., 1998; Woolliams et al.,

Received February 18, 2021.

Accepted June 10, 2021.

*Corresponding author: Mekonnen.HaileMariam@agriculture.vic.gov.au

2015); however, they are difficult to implement due to the dispersed structure of dairy cattle breeding (Howard et al., 2017). Typically, several elite nucleus herds supply breeding stock to the global industry, which, coupled with an intense marketing of elite bulls by AI companies, has led to favoring short-term genetic gain over strategies that aim to control inbreeding. Maximizing diversity through a well-designed RP could be an alternate strategy worth considering. A poorly designed RP can result in bias in genomic EBV (**GEV**; Dassonneville et al., 2012) because animals more related to the RP have higher prediction accuracies than less-related animals. Individuals less related to the RP are more likely to be regressed to the mean, resulting in lower reliability and are therefore less likely to be selected as parents of the next generation.

Inclusion of females into the RP has been shown to improve the accuracy of prediction (Calus et al., 2013). Large-scale incorporation of females into the Australian genomic RP observed an increase in the reliability of genomic breeding values of young bulls (5.8 and 2.5% for Holstein and Jersey) and cows (5–7% for Holsteins and between 2 and 3% for Jerseys; (Pryce et al., 2012, 2018). This genomic RP, known as genomic information nucleus herds (**GInfo**) in Australia, comprises herds with excellent recorded data (especially for fertility and other low heritability traits) from all dairy regions in the country, with genotyping of the GInfo cows having started routinely in 2013. The RP, such as GInfo, need to be continuously updated through the addition of new females representative of all selection candidates to potentially capture more diverse pedigrees than male reference populations (Pszczola and Calus, 2015). Thus, female reference populations may play an important part in GS strategies through contributing to data for (1) prediction accuracy and (2) population diversity.

In this study we aimed to quantify and compare changes in genetic gain and diversity resulting from GS in Australian Holstein and Jersey cattle populations [including cattle from GInfo; the Australian National Herd (**NatHerd**), which is not part of GInfo; and bulls]. Coancestry between cow populations was quantified and rates of inbreeding and genetic gain pre- and post-genomic selection implementation were investigated. To determine the rates of change in genetic diversity, we compared relative changes of pedigree and genomic inbreeding. To determine the rate of genetic gain, we compared the relative change in the national selection index [known as Balanced Performance Index (**BPI**)], a trait of moderate heritability (protein) and a trait of low heritability (fertility). We explored how these changes could explain the differences observed between breeds and populations.

MATERIALS AND METHODS

Animals and Pedigree Data

The data for this study were extracted from the DataGene database (Melbourne, Australia) from the official December 2019 genetic evaluation run. A total of 2,330,579 Holstein and Jersey animals were born between 2000 and 2019. These animals had both EBV and at least one generation of pedigree (i.e., at least 2 known parents). Using a subset of females from the datafile, we accessed cows that were part of (1) GInfo, 157,584 cows from 103 herds, and (2) NatHerd, 2,056,333 cows from 7,837 herds. Cows that were not part of GInfo are referred to as NatHerd in this paper.

The EBV included the BPI [the main economic index used for selection in Australia since 2016; see Byrne et al. (2016) for further details], protein yield, and fertility EBV; the units of these EBV are AU\$, kg, and fertility EBV 6-wk in-calf rate (expressed as a deviation from the mean of 100), respectively. Only bulls registered for artificial breeding services were considered for these analyses. Analysis was done within breed.

Animals were identified as either Holstein or Jersey (i.e., using a 4-letter breed code available on each animal from DataGene; FFFF or JJJJ). The first 2 letters correspond to the sire breed and the second 2 to the dam breed, for example, an animal with a breed code of FFJJ has a Holstein sire and a Jersey dam.

Pedigree Completeness. As inbreeding estimates are known to be sensitive to pedigree completeness, only animals with at least 87.5% of recorded ancestors traced back 3 generations were used for this study. Pedigree completeness was evaluated using complete generation equivalents, which is the weighted sum of generations over all known ancestors. The weighting of the terms was $(1/2)^n$ where n is the number of generations separating the individual to each known ancestor (Maignel et al., 1996). As a result of the pedigree completeness criterion, approximately 33% of Holstein cows and 37% of Jersey cows were removed. Table 1 shows the mean numbers of generations traced back for the final (analysis) data calculated using the *pedigree* function version 1.4 in R (<https://CRAN.R-project.org/package=pedigree>). Table 2 shows the number of cows in the pedigree data set after each editing criteria. As we used a subset of bulls registered for artificial breeding, which have undergone prescreening for pedigree completeness, almost all of them passed the edits and are not presented.

Genotype Data. A subset of the cow population from both GInfo and NatHerd have genotype data. Although most cows in GInfo herds (approximately 60%)

Table 1. Mean number (\pm SD) of generations traced back for the national herd (NatHerd), genomic reference population (GInfo), and bulls for Holsteins and Jerseys

Item	Holstein	Jersey
NatHerd	11.8 \pm 2.69	9.76 \pm 1.68
GInfo	12.9 \pm 2.74	10.3 \pm 1.76
Bulls	13.4 \pm 3.33	9.96 \pm 1.73

are genotyped, only 30% of the cows in NatHerd were genotyped. Genotyping of cows is an individual decision for farmers, and it is likely that in the NatHerd data set there is a bias toward high genetic merit animals being genotyped.

A total of 139,898 genotyped individuals were available for Holsteins, Jerseys, and their crosses from DataGene. Genotyping is done by commercial providers which is then submitted to DataGene. DataGene imputes the genotype data to a standard set of 45,685 SNP genotypes for routine evaluations (Nieuwhof et al., 2010), where on average there is one SNP every 54.8 \pm 52.9 kb. Before imputation, the genotypes of these animals underwent standard quality control used by DataGene Limited (e.g., Nieuwhof et al., 2010), where SNPs were screened based on an average call rate (>0.9), average genotrain score (>0.6), minor allele frequency (MAF > 0.01), and a Hardy-Weinberg statistic (<600). Data from SNPs that did not meet these criteria were removed.

The breed of genotyped cows (i.e., Holstein or Jersey) was validated using the ADMIXTURE program (Alexander et al., 2009). Two ancestral breed populations were defined ($k = 2$; Holstein and Jersey as identified by DataGene through farmer records) and the likelihood that a given proportion of all markers came from either population, based on a postulated allele frequency for each marker in both populations was calculated. Individuals whose likelihood of their markers being from a given breed exceeded 0.8 were considered to belong to the selected breed population. When determining breeds using ADMIXTURE, we found approximately 2.9% of Holsteins and 1.4% of Jerseys were incorrectly identified as purebred animals when

they were crossbred (defined as <0.8 of either breed by ADMIXTURE), whereas 5.7 and 4.4% of Holsteins and Jerseys, respectively, were incorrectly classified as nonpurebred animals when they were purebred.

After correcting the breed information based on these findings, 114,567 Holsteins and 17,352 Jerseys animals were available for subsequent analysis. The Holstein data set had 17,080 bulls and 73,003 cows, whereas the Jersey data set had 2,737 bulls and 11,890 cows born between 2000 and 2017. Figure 1 shows the number of genotyped cows by birth year, pedigree completeness, herd group (cows), and breed.

Generation Interval and Age of Sires. As generation interval is a key driver of the rate of genetic gain, the age of sires when their progeny were born is an important statistic when assessing genetic progress per year in dairy cattle. The average age of sires was defined as the mean difference between the birth date of an individual and its sire, in years or fraction thereof. An individual with a sire that was less than 18 mo of age when they were born was removed, as semen collection under 9 mo is unlikely (assuming a 9-mo gestation period). This edit removed 284 cows. The upper limit was defined as k standard deviations greater than the mean for the difference in age between sire and offspring. Observations that were above the upper limit were removed, where $k = |\Phi^{-1}(1/n)|$, n is the number of data records, and $\Phi^{-1}(\cdot)$ is the inverse cumulative distribution function of a standard normal distribution (Aggarwal, 2013). As a result, cows where their sire was more than 20.7 yr old in Jerseys and 23.7 yr in Holsteins were removed. This edit removed 2,288 Holsteins and 182 Jerseys.

Measures of Inbreeding and Genetic Diversity

Pedigree-Based Measures at Individual Level.

Individual pedigree inbreeding coefficients (F_{PED}) were calculated from all available pedigree data according to (VanRaden, 1992), these were estimated using the PEDIG package developed by Boichard (2002).

Pedigree-Based Measures at Herd Level. To determine if the GInfo population is genetically rep-

Table 2. Number of cows in the pedigree data set (numbers in the genomic information nucleus are shown in parentheses)

Item	Holstein	Jersey
Total animals in pedigree file with known sire	2,156,087	310,790
At least 3 generations of complete pedigree	1,450,369	196,540
Breeding values	1,129,367	150,766
BPI ¹ and protein reliability $>35\%$	917,190 (80,637)	123,980 (13,162)
Fertility reliability $>35\%$	789,311 (74,865)	105,010 (12,190)

¹BPI = Balanced Performance Index.

representative of the wider national herd, within- and between-herd relationships were calculated. To ensure fair comparisons, we chose a cohort of cows born in a single year (2017), which represented the largest recent group of animals. An additive relationship matrix was calculated using the `makeA` function in the “pedigree” package version 1.4 from R (R Core Team, 2020; <https://CRAN.R-project.org/package=pedigree>). Herd coancestry was calculated as the mean of individuals coancestry coefficients within a herd, or mean coancestry of individuals between herds. In all calculations, the relationship of an animal to itself was ignored. For these calculations, we selected herds with a minimum of 10 Jersey animals and 30 Holstein animals. The data used for the final analysis included 42,046 Holsteins cows from 430 herds (66 GInfo herds) and 6,424 Jerseys cows from 145 herds (19 GInfo herds).

Genomic-Based Measures

Genomic inbreeding coefficients were calculated using 2 different methods; the first was runs of homozygosity (ROH), which represent the autozygous segments of

the genome and the second using a marker-by marker approach to calculate the excess of homozygosity.

An ROH was defined as a homozygous segment of at least 35 SNP or 1,000 kb long, with at least one SNP per 75 kb. Two consecutive SNP could not be included if they were more than 250 kb apart. The ROH were identified using the PLINK “`homozyg`” function (Purcell et al., 2007; command link: `plink-cow-bfile genotyping_data_filename-homozyg-homozyg-kb 1000-homozyg-snp 35-homozyg-window-snp 35-homozyg-window-density 75-homozyg-gap 250-out output_filename`). We tested sliding windows sizes of 20, 35, and 50 and found that 35 was most correlated with other inbreeding measures. This is consistent with Lencz et al. (2007) who suggested using a sliding window of 36 for Jerseys and 39 for Holsteins. Based on these settings, the number of generations we were able to trace back was 10 to 15 generations (Thompson, 2013).

The ROH-based inbreeding estimates, $F_{ROH,i}$ were computed as the proportion of the genome included in the ROH as follows:

$$F_{ROH,i} = \frac{\sum L_{ROH,i}}{L_{auto}}$$

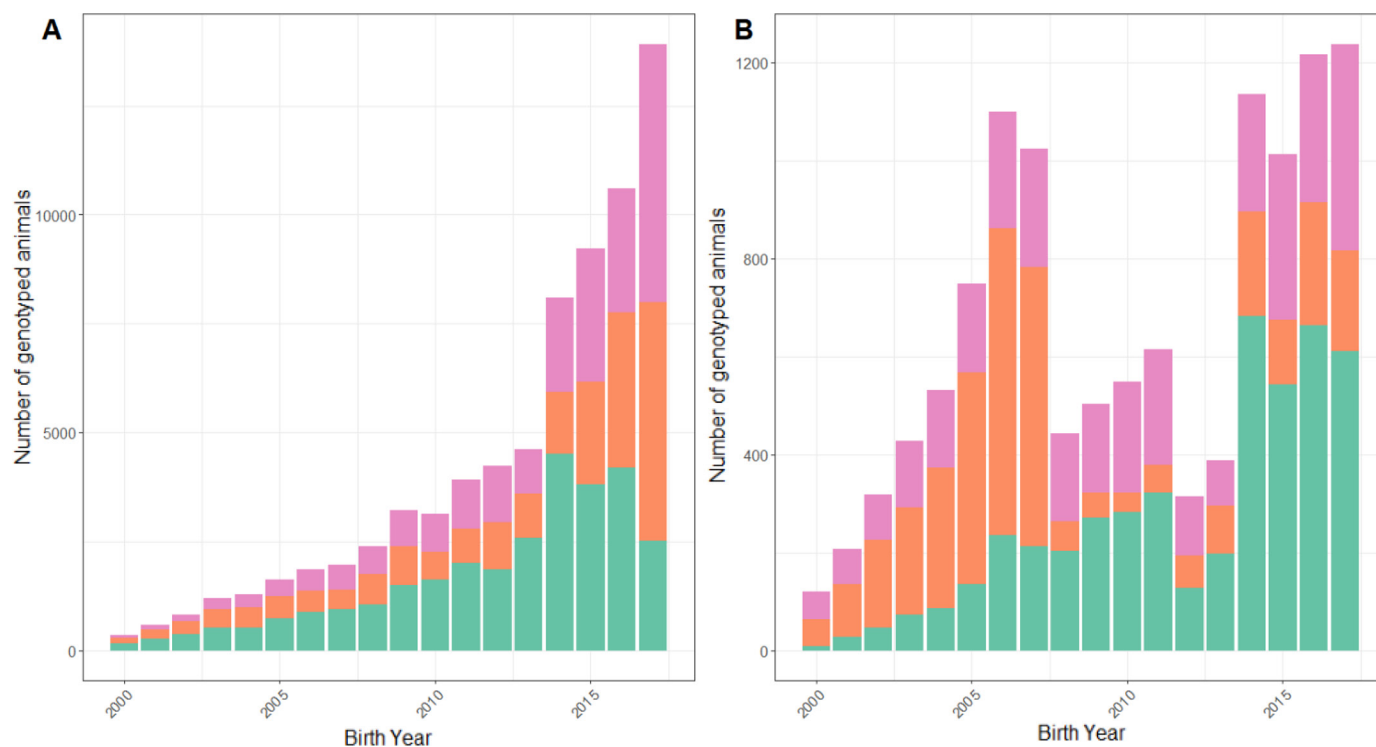


Figure 1. Distribution of genotyped cows by year of birth from 2000 to 2017 for Holsteins (A) and Jerseys (B) that are in the genomic information nucleus (green), are in the national herd with pedigree and genomic information (orange), or are genotyped but have insufficient pedigree records (pink).

where $\Sigma L_{ROH,i}$ is the total length of ROH for individual i , and L_{auto} is the length of the autosome genome covered by SNPs after withholding gaps longer than 250 kb between 2 SNPs, corresponding to the length of the autosomal genome on which ROH can be detected. This parameter allowed for the detection of ROH on 87.6% of the autosomal genome.

The mean length of the ROH was reported for each individual and was defined as

$$L_{ROH,mean,i} = \frac{\Sigma L_{ROH,i}}{N_{ROH,i}},$$

where $\Sigma L_{ROH,i}$ is the total length of ROH for individual i in kb and $N_{ROH,i}$ is the total number of ROH for individual i .

For animals where there is selective mating (i.e., dairy cattle), there is likely to be more homozygosity than expected as some alleles or haplotypes are under intense selection, therefore we used a measure that deliberately examines excessive homozygosity (compared with expectation). Calculation of inbreeding based on excess homozygosity was implemented within breed using the PLINK “*het*” function (Purcell et al., 2007) and defined as

$$F_{HOM} = \frac{O - E}{N - E},$$

where O is the observed number of homozygous markers of the individual, E is the expected number of homozygous markers under the Hardy-Weinberg equilibrium calculated from the allele frequencies estimated on the sample, and N is the total number of SNPs.

Pearson’s product-moment correlations between the pedigree and genomic methods were computed for each breed and cow population to assess the similarity between them. The approach of VanRaden (2008) was used to make genomic measures (**G**) comparable to pedigree (**A**), coefficients of **G** were adjusted for regression of **G** on **A** and used to assess if genomic **F** can be used to gauge **F** for ungenotyped animals.

Impact of Genomic Selection on Genetic Gain and Genetic Diversity. To assess the effect of GS on genetic diversity and genetic gain in the national herd, GInfo or the bull population, we used the method of Doublet et al. (2019), implementing the following linear model using the R (version 3.6.1) function *lm* (<https://www.r-project.org>):

$$Y_i = \left\{ \begin{array}{l} a_1 + b_1 \cdot x_i + e_i, \quad 2000 \leq x_i \leq 2012 \\ a_2 + (b_1 + \delta) \cdot x_i + e_i, \quad 2013 \leq x_i \leq 2017 \end{array} \right\},$$

where Y_i is the variable of interest i (BPI, protein EBV, and fertility EBV for genetic gain and F_{PED} , F_{ROH} , and F_{HOM} for genetic diversity), a_i is the intercept, x_i is the birth year of the cow or bull i , and b_1 is the associated regression coefficient, if cow or bull i was born between 2000 and 2012 (pregenomics) or $b_1 + \delta$ if born between 2013 and 2017 (GS). The effect of GS was measured with the δ coefficient and is the difference in genetic gain pre- and postimplementation of genomic selection. Its significance was tested with an ANOVA.

The relative change (**RC**) of the slopes of regression before and after GS was computed as

$$RC = \frac{\delta}{|b_1|}.$$

Effect of Genomic Selection on Inbreeding. To assess if GS resulted in increased genetic gain per unit increase in inbreeding, the slope of regression for each trait was divided by the slope of genomic inbreeding (F_{ROH}) for the 2 time periods, pregenomics and GS. The difference and RC were then calculated.

RESULTS

In both breeds, GInfo had more complete pedigrees than the NatHerd (average number of generations was 12.9 vs. 11.8 Holsteins and 10.3 vs. 9.8 Jerseys; Table 1). In Holsteins, bulls had the most complete pedigree, then GInfo and the NatHerd. In Jerseys, GInfo animals had greater pedigree completeness than bulls (10.3 vs. 9.96).

The number of bulls with genomic data has increased considerably since 2010. For bulls born in 2017, 3,370 Holstein and 442 Jersey were genotyped. In 2017, 11 and 9% of Holstein and Jersey genotyped bulls, respectively, entered AI. The number of bulls registered for AI has increased in Holsteins under GS from 2010 to 2017 (200 to 340 respectively) and has remained similar for Jerseys (37 to 40). The number of cows with genotype data by breed and subpopulation is shown in Figure 1. The number of genotyped Holstein females has increased 4-fold in 2017 when compared with 2016 from 3,152 to almost 14,000. A large proportion of these animals were from the national herd (i.e., not participants of GInfo). In Jerseys, there are 2 peaks in the number of animals genotyped: the first in 2007 and the second

in 2015 coinciding with 2 large research projects that funded genotyping. Genotyping of Jerseys appears to have reached a plateau over the last 3 years of the data (2015–2017) with around 50% of genotyped Jerseys in this period being GInfo animals. Seventy-four percent of Holsteins and 69% of Jersey genotyped cows had at least 3 generations of complete pedigree.

Effect of Genomic Selection on Generation Interval and Genetic Gain

As expected, GS has reduced the mean difference between the birth date of a sire and its progeny, which, in the period under observation, peaked at approximately 7.5 yr in 2009 (Figure 2). Since 2009, there has been a considerable decrease in the mean age of sires for Holsteins in both GInfo and national herds, as in 2017 it was 5.4 and 5.7 yr, respectively. We also observed similar trends in GInfo Jerseys, which peaked at 7.6 yr in 2009 and decreased to 6.2 yr in 2017. For Jerseys in the NatHerd, the average age of sires was more variable and estimated to be on average 6.8 yr in the pregenomic period and 6.9 yr under GS.

Due to a reduction in generation interval (Figure 2), the rates of genetic gain in Holsteins and Jerseys have increased in recent years with the implementation of GS in 2011 in Australia. The GInfo herds had greater rates of genetic gain in BPI after the introduction of GS. Table 3 and Table 4 show that the total genetic merit index (BPI) increased at a higher rate in both Holsteins and Jerseys cows under GS. In Holsteins, we observed increases of between 0.07 and 0.09 genetic standard deviation (GSD) units per year for the BPI (\$7–\$9 BPI units per year). In Jersey cows, we saw increases of 0.04 and 0.06 GSD units per year for BPI (\$4.4 and \$6 for BPI per year) in the national herd and GInfo populations respectively. In Jersey bulls, GS appears to have resulted in a slower rate of genetic gain than in the pregenomic period (Table 4). The GInfo herd has had similar or higher rates of genetic gain in BPI compared with the national herd for both Jerseys and Holsteins breeds (Figure 3). The rate of genetic gain is consistent with this observation where Holstein bulls had a higher mean BPI than Jerseys. However, surprisingly, the RC (defined as the difference between the 2 time periods divided by the pregenomic genetic gain rate) was lower in the bulls compared with Holstein cows (0.52 vs. 1.63 and 1.61; Table 3) post-GS.

The traits included in the BPI show similar patterns in terms of genetic gain. The introduction of GS (from 2011) has resulted in increases in genetic gain for protein yield in Holstein bulls and cows in the national

herd (0.02 GSD/yr and 0.04 GSD/yr; Table 3) and all Jersey cows (0.04–0.05 GSD/yr), but a decreased rate for Jersey bulls (–0.08 GSD/yr, Table 4).

The rate of genetic gain in the fertility EBV had the highest RC and was 5.4 times and 6 times greater when comparing pregenomic selection (2000–2012) to postgenomic selection (2013–2017) in Holstein cows in the NatHerd and GInfo, respectively (Table 3). Before the introduction of GS, the rate of genetic gain for fertility per year was declining in both the national herd (–0.02) and GInfo population (–0.02) in Holsteins. In the period from 2013 to 2017, the rate of genetic gain in the fertility EBV has increased to 0.08 and 0.12 GSD units per year (Table 3). In Jerseys, fertility rates in the national herd have decreased significantly (–0.03 GSD/yr; RC –8.67), did not change in GInfo (0.37, NS) and increased in the bull population (RC 4.19; Table 4).

Pedigree Inbreeding

Annual rates of pedigree inbreeding have been increasing in both breeds and subpopulations. The GInfo herds have historically had higher levels of inbreeding in both Holsteins and Jerseys (Figure 3). Pedigree-based inbreeding rates increased after the introduction of GS (2013–2017) in the national herd for both Holsteins and Jerseys compared with the pregenomics period (2000–2012; Table 3 and Table 4). The GInfo Jersey cows had the largest increase within the cow populations, doubling the rate of inbreeding since GS. The largest increase in the rate of inbreeding was seen in Holstein bulls where the rate of inbreeding was 20 times higher after GS than it was in the pregenomics period (0.037 to 0.760% per year, Table 3). In Jersey bulls, it was 5 times higher (0.037 to 0.18% per year, Table 4).

Herd Coancestry

Jerseys were more related to their herd mates (using pedigree) and Jersey herds were also more related to other herds when compared with Holsteins (Table 5). The mean coancestry coefficients were highest within-herd for both GInfo and the national herd, 0.11 and 0.15 for Holsteins and Jerseys, respectively. The GInfo herds were similarly related to each other as they were to the national herd (0.07–0.08 and 0.10–0.11 for Holsteins and Jerseys, respectively). There was a slight tendency for national herds to be less related to each other than GInfo herds (0.07 and 0.09 for Holsteins and Jerseys, respectively).

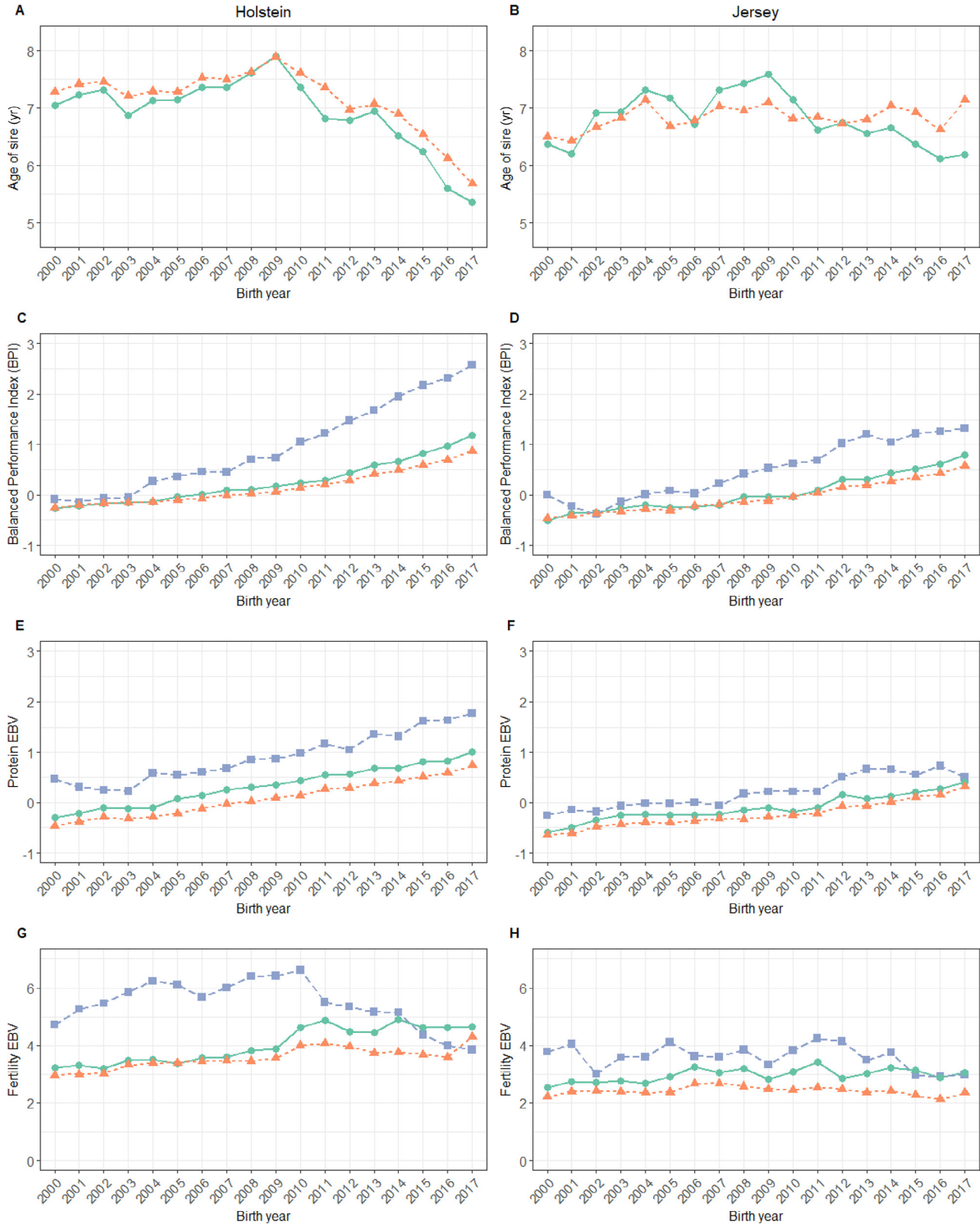


Figure 2. Average age of sires when progeny was born (A, B) by year of birth of the progeny, mean Balanced Performance Index (C, D), protein EBV (E, F), and fertility EBV (G, H) by birth year for the female genomic reference population (GInfo), national herd, and bulls for Holsteins and Jerseys. The orange lines with triangles represent the GInfo population, the green lines with circles represent the national herd, and the purple lines with squares represent the bulls registered for artificial breeding.

Table 3. Rates of genetic gain for the Balanced Performance Index (BPI), protein EBV, fertility EBV (expressed in units of approximate genetic SD¹), and pedigree inbreeding (F_{PED}) in Holstein cows in the national herd (NatHerd), genomic reference (GInfo), and bull populations²

Parameter	Population	No. of animals 2000–2012	No. of animals 2013–2017	<i>b</i> ₁ (±SE)	<i>b</i> ₂ (±SE)	δ	<i>P</i> -value of δ	RC
BPI	NatHerd	681,439	155,114	0.04 (±0)	0.11 (±0)	0.07	0	1.63
	GInfo	52,913	27,724	0.06 (±0)	0.15 (±0)	0.09	0	1.61
	Bulls	5,001	1,996	0.13 (±0)	0.22 (±0.01)	0.08	0	0.64
Protein EBV	NatHerd	681,439	155,114	0.06 (±0)	0.08 (±0)	0.02	0	0.35
	GInfo	52,913	27,724	0.07 (±0)	0.08 (±0)	0	0	0.03
	Bulls	5,001	1,996	0.07 (±0)	0.11 (±0.01)	0.04	1.58e-260	0.6
Fertility EBV	NatHerd	596,810	117,636	−0.02 (±0)	0.08 (±0)	0.1	0	5.4
	GInfo	49,978	24,887	−0.02 (±0)	0.12 (±0)	0.15	0	6.06
	Bulls	4,999	1,987	0.06 (±0)	0.08 (±0.01)	0.02	1.54e-252	0.31
F _{PED} ³ (in %)	NatHerd	681,439	155,114	0.11 (±0)	0.12 (±0)	0.02	0	0.15
	GInfo	52,913	27,724	0.11 (±0)	0.14 (±0.01)	0.03	0	0.33
	Bulls	5,001	1,996	0.04 (±0.01)	0.78 (±0.04)	0.74	0	20.35

¹Published SD of EBV from DataGene (accessed December 2019) were 107.4, 10.9, and 6.3 for BPI, protein, and fertility, respectively.

²*b*₁ is the slope of regression of each parameter depending on birth year for animals born between 2000 and 2012 (pregenomics); δ is the difference between the slopes of regression of each parameter depending on birth year for 2000–2012 and 2013–2017 (genomic selection) for animals in NatHerd, GInfo, or bulls; *b*₂ is the slope of the parameter or animals born in the genomic selection era (2013–2017), equal to *b*₁ + δ. The relative change (RC) is equal to $\frac{\delta}{|b_1|}$.

³Slopes and SE are displayed in %; *P*-values and relative changes are not.

Genomic Inbreeding

Jersey cows have a higher mean F_{ROH} and shorter mean ROH length, thus older inbreeding compared with Holsteins cows (Figure 4A–D). The rate of ROH-based inbreeding in cows was greater under GS; however, the magnitude of the increase is less than that of bulls. For F_{ROH} in Holstein cows (GInfo and NatHerd) we observed similar fold increases (0.44 vs. 0.56; Table

6). Similarly, F_{ROH} increased in Jersey cow populations, whereas it was higher in the GInfo population (Table 7). In Holstein and Jersey bulls, ROH-based inbreeding increased significantly after GS compared with pregenomics, i.e., from 0.17 to 0.99% per year in Holsteins and 0.23 to 0.40% per year in Jerseys with RCs of 4.95 and 0.75, respectively (Tables 6 and 7).

The mean ROH length had larger increases in the GInfo Holsteins than the NatHerd. The mean ROH

Table 4. Rates of genetic gain for Balanced Performance Index (BPI), protein EBV, fertility EBV (expressed in units of approximate genetic SD¹), and pedigree inbreeding (F_{PED}) in Jersey cows in the national herd (NatHerd), genomic reference (GInfo), and bull populations²

Parameter	Population	No. of animals 2000–2012	No. of observations 2013–2017	<i>b</i> ₁ (±SE)	<i>b</i> ₂	δ (±SE)	<i>P</i> -value of δ	RC
BPI	NatHerd	87,610	23,208	0.05 (±0)	0.09 (±0)	0.04	0	0.96
	GInfo	8,566	4,596	0.05 (±0)	0.11 (±0.01)	0.06	0	1.1
	Bulls	848	232	0.1 (±0.01)	0.04 (±0.03)	−0.06	2.20e-50	−0.59
Protein EBV	NatHerd	87,610	23,208	0.04 (±0)	0.09 (±0)	0.05	0	1.29
	GInfo	8,566	4,596	0.04 (±0)	0.08 (±0.01)	0.04	9.43e-157	0.9
	Bulls	848	232	0.05 (±0.01)	−0.03 (±0.03)	−0.08	9.71e-20	−1.63
Fertility EBV	NatHerd	76,324	16,596	0 (±0)	−0.03 (±0)	−0.03	7.05e-161	−8.98
	GInfo	7,979	4,111	−0.01 (±0)	−0.01 (±0.01)	0	2.50e-31	0.33
	Bulls	848	220	−0.03 (±0.01)	0.09 (±0.04)	0.12	0.219	4.39
F _{PED} ³ (in %)	NatHerd	87,610	23,208	0.08 (±0)	0.09 (±0.01)	0.01	9.46e-144	0.17
	GInfo	8,566	4,596	0.08 (±0.01)	0.16 (±0.02)	0.08	3.04e-56	1.05
	Bulls	848	232	0.04 (±0.02)	0.16 (±0.14)	0.13	6.77e-07	3.6

¹Published SD of EBV from DataGene (accessed December 2019) were 100.7, 12.4, and 3.9 for BPI, protein, and fertility, respectively.

²*b*₁ is the slope of regression of each parameter depending on birth year for animals born between 2000 and 2012 (pregenomics); δ is the difference between the slopes of regression of each parameter depending on birth year for 2000–2012 and 2013–2017 (genomic selection) for animals in the national herd (NatHerd), genomic reference population (GInfo), or bulls; *b*₂ is the slope of the parameter or animals born in the genomic selection era (2013–2017), equal to *b*₁ + δ. The relative change (RC) is equal to $\frac{\delta}{|b_1|}$.

³Slopes and SE are displayed in %. *P*-values and relative changes are not.

Table 5. Mean pedigree coancestry within and between the national herd (NatHerd) and genomic reference (GInfo) populations for Holsteins and Jerseys cows born in 2017¹

Parameter	Holstein	Jersey
Within-herd GInfo	0.11 (0.02)	0.15 (0.03)
Between-herd GInfo	0.08 (0.01)	0.11 (0.03)
Between-herd GInfo and NatHerd	0.08 (0.01)	0.10 (0.03)
Between-herd NatHerd	0.07 (0.02)	0.09 (0.03)
Within-herd NatHerd	0.11 (0.02)	0.15 (0.03)

¹Values are mean \pm SE.

length after GS increased 17.2 kb and 11.5 kb in Holstein and Jersey GInfo populations, whereas there was only a small increase in the mean ROH length in the NatHerd for both breeds. Changes in the excess of homozygosity were greater in Jersey cows than in Holsteins (Figure 4E and F).

In the subset of cows with genotype data, we observed greater rates of pedigree inbreeding. In genotyped Holsteins, the rate of inbreeding and rate of relative change was greater for genomic (F_{ROH} and F_{HOM}) than pedigree estimates of inbreeding, except for F_{HOM} GInfo, where less homozygosity than expected was observed after the introduction of GS (Table 8). This decrease in slope was also observed in all genotyped Holstein cows (0.194–0.183; Table 8). In Jerseys, the rates of genomic inbreeding are higher than that of pedigree inbreeding. In the national herd, genomic inbreeding has doubled since GS, whereas in GInfo, the changes in the rate of inbreeding are not as large (Table 9).

Differences in the average inbreeding coefficients within subpopulations can be found in Supplemental Figure S1 (<https://doi.org/10.6084/m9.figshare.15153495.v2>). The Pearson correlation coefficients

between pedigree and genomic inbreeding calculations per year of birth are presented in Figure 5. Correlations between pedigree and genomic inbreeding calculations ranged from 0.52 to 0.75 with the correlations in bulls being slightly greater than for cows. In cows and Holstein bulls, F_{PED} had a higher correlation with F_{ROH} than F_{HOM} . The correlation between both genomic measures (F_{ROH} and F_{HOM}) was strong (>0.89).

Genetic Gain Per Unit of Inbreeding

Genomic selection has resulted in a greater genetic gain in BPI per unit of inbreeding in Holsteins and Jerseys cows (RC 0.62–0.74; Table 10). In bulls, there is a greater amount of inbreeding per unit increase in the BPI for both breeds. Increases in inbreeding per unit of gain in protein EBV were observed in all Holstein populations and Jersey bulls post GS, whereas in Jersey cows, we observed more genetic gain for protein per unit of inbreeding. In Holsteins cows and GInfo Jerseys, fertility EBV appears to have improved when compared with the change in inbreeding over the same period (Table 10), whereas inbreeding is accumulating faster under GS per unit of genetic gain in the fertility EBV in Jerseys in the NatHerd.

DISCUSSION

Genomic selection has had a profound effect on the rate of genetic gain in crop and animal species worldwide (e.g., Heffner et al., 2010; García-Ruiz et al., 2016). Dairy was one of the first industries to widely adopt the technology, and in Australia, genomic EBV have been part of selection decisions since 2011. Results

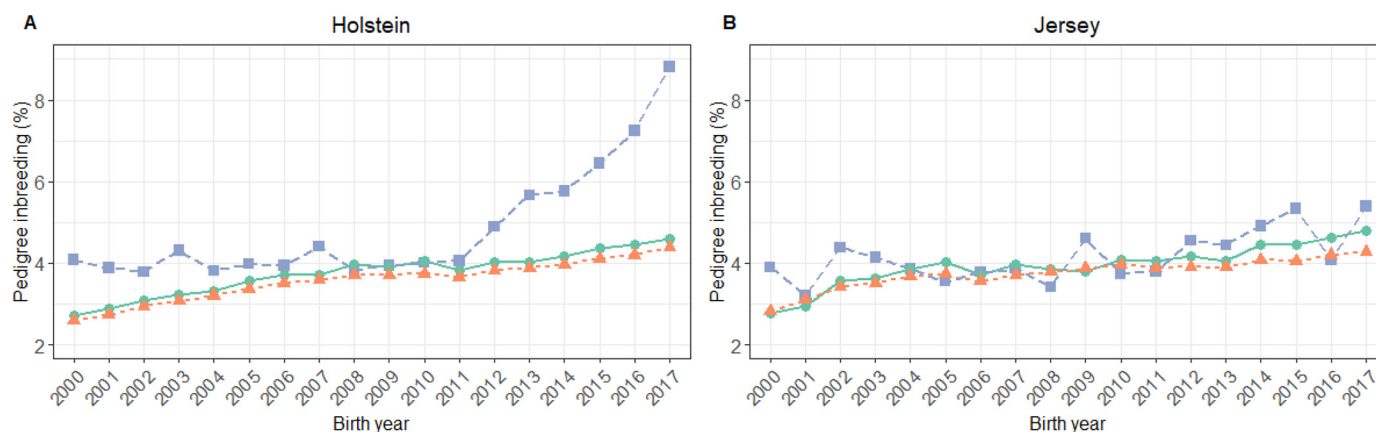


Figure 3. Average pedigree inbreeding coefficients (%) for Holsteins and Jerseys bulls, females in the genomic reference population (GInfo), and the national herd. The orange lines with triangles represent the GInfo population, the green lines with circles represent the national herd, and the purple lines with squares represent the bulls registered for artificial breeding.

from this study have shown that when comparing pre- and postgenomic selection, the rate of genetic gain in BPI has increased by ~160% in Holstein females and ~100% in Jersey females and is comparable to results from the United States and France (García-Ruiz et al.,

2016; Doublet et al., 2019). This has been accompanied by increasing rates of inbreeding.

This paper aimed to compare changes in genetic gain and inbreeding due to GS, applied within Australian dairy subpopulations for Holstein and Jersey cattle.

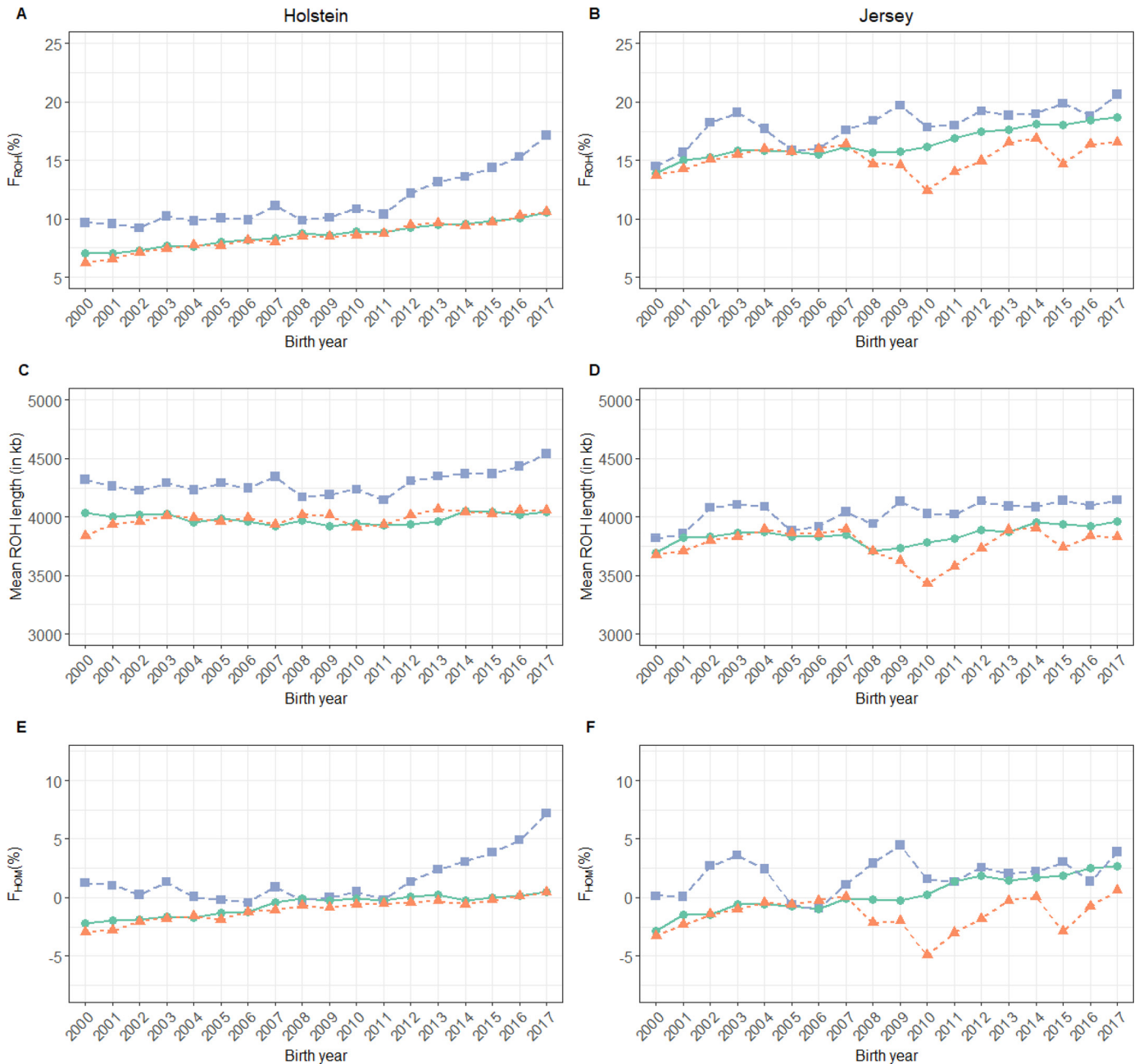


Figure 4. Genomic trends of diversity in bulls and females in the genomic reference population (GInfo) and the national herd. (A, B) Inbreeding based on runs of homozygosity (F_{ROH}); (C, D) mean runs of homozygosity (ROH) length; and (E, F) excess of homozygosity (F_{HOM}) for Holsteins and Jerseys. The orange lines with triangles represent the GInfo population, the green lines with circles represent the national herd, and the purple lines with squares represent the bulls registered for artificial breeding.

Table 6. Average rates of genomic inbreeding per year of birth for Holstein cows in the national herd (NatHerd), genomic reference (GInfo), and bull populations¹

Parameter	Population	No. of animals 2000–2012	No. of animals 2013–2017	b_1 (\pm SE)	b_2 (\pm SE)	δ	P -value of δ	RC
F_{ROH}^2 (in %)	NatHerd	11,146	25,577	0.21 (\pm 0.01)	0.33 (\pm 0.02)	0.12	0	0.56
	GInfo	15,406	20,874	0.18 (\pm 0.01)	0.25 (\pm 0.02)	0.08	0	0.44
	Bulls	2,590	1,739	0.17 (\pm 0.01)	0.99 (\pm 0.06)	0.82	0	4.95
Mean ROH length	NatHerd	11,146	25,577	1.76 (\pm 1.58)	1.92 (\pm 2.3)	0.16	1.83e-40	0.09
	GInfo	15,406	20,874	-7.49 (\pm 1.37)	10.23 (\pm 2.46)	17.72	7.14e-49	2.37
	Bulls	2,590	1,739	-4.04 (\pm 2.36)	46.25 (\pm 7.05)	50.29	5.42e-29	12.44
F_{HOM}^2 (in %)	NatHerd	11,146	25,577	0.18 (\pm 0.01)	0.29 (\pm 0.02)	0.1	1.05e-161	0.57
	GInfo	15,406	20,874	0.2 (\pm 0.01)	0.1 (\pm 0.02)	-0.09	3.67e-53	-0.47
	Bulls	2,590	1,739	-0.02 (\pm 0.02)	1.17 (\pm 0.07)	1.2	1.16e-204	51.59

¹ b_1 is the slope of regression of each parameter depending on birth year for animals born between 2000 and 2012 (pregenomics); δ is the difference between the slopes of regression of each parameter depending on birth year for 2000–2012 and 2013–2017 (genomic selection) for animals in the national herd (NatHerd), genomic reference population (GInfo), or bulls; the relative change (RC) is equal to $\frac{\delta}{|b_1|}$; b_2 is the slope of the parameter or animals born in the genomic selection era (2013–2017), equal to $b_1 + \delta$.

²Slopes and SE are displayed in %; P -values and relative changes are not. F_{ROH} = inbreeding based on runs of homozygosity; ROH = runs of homozygosity; F_{HOM} = inbreeding based on excess homozygosity.

In both breeds, the GInfo showed similarities to the NatHerd for both herd diversity and inbreeding trends. However, the GInfo populations were genetically more advanced (higher mean BPI) than the NatHerd populations but showed similar fold increases in genetic gain before and after implementation of GS.

A greater rate of genetic gain and decrease in the mean age of sires compared with when daughters were born was observed in GInfo compared with NatHerd and is most likely to be the result of early adoption of GS. In Holsteins, the greatest effect on both inbreeding and genetic gain was first observed in bulls (which have greater selection intensity), followed by GInfo cows and cows in the NatHerd. Although the genetic diversity

and genetic gain in GInfo and NatHerd were similar for Jerseys, it should be noted that Jersey populations had less herd diversity and limited use of young Jersey bulls in the NatHerd.

Rate of Genetic Gain

Early predictions expected GS in dairy cattle to increase the annual genetic gain by between 70 and 108% depending on the breeding scheme implemented (Hayes et al., 2009; de Roos et al., 2011). The current study found that GS has doubled the rate of annual genetic gain for BPI in cows, whereas the response in bulls was varied. These findings are greater than those observed

Table 7. Average rates of genomic inbreeding per year of birth for Jersey cows in the national herd (NatHerd), genomic reference (GInfo), and bull populations¹

Parameter	Population	No. of animals 2000–2012	No. of animals 2013–2017	b_1 (\pm SE)	b_2 (\pm SE)	δ	P -value of δ	RC
F_{ROH}^2 (in %)	NatHerd	4,024	1,824	-0.06 (\pm 0.02)	0.05 (\pm 0.09)	0.1	3.63e-09	1.89
	GInfo	2,875	3,167	0.16 (\pm 0.03)	0.23 (\pm 0.05)	0.06	2.29e-113	0.4
	Bulls	481	201	0.23 (\pm 0.05)	0.4 (\pm 0.21)	0.17	8.99e-08	0.75
Mean ROH length	NatHerd	4,024	1,824	-15.93 (\pm 2.52)	-14.12 (\pm 7.24)	1.81	0.053	0.11
	GInfo	2,875	3,167	-3.83 (\pm 2.6)	7.66 (\pm 4.78)	11.49	6.53e-45	3
	Bulls	481	201	13.52 (\pm 4.9)	13.38 (\pm 18.17)	-0.14	0.002	-0.01
F_{HOM}^2 (in %)	NatHerd	4,024	1,824	-0.09 (\pm 0.03)	0.31 (\pm 0.11)	0.39	0.006	4.48
	GInfo	2,875	3,167	0.28 (\pm 0.03)	0.33 (\pm 0.06)	0.05	1.92e-63	0.18
	Bulls	481	201	0.11 (\pm 0.06)	0.36 (\pm 0.26)	0.25	0.021	2.18

¹ b_1 is the slope of regression of each parameter depending on birth year for animals born between 2000 and 2012 (pregenomics); δ is the difference between the slopes of regression of each parameter depending on birth year for 2000–2012 and 2013–2017 (genomic selection) for animals in the national herd (NatHerd), genomic reference population (GInfo), or bulls; the relative change (RC) is equal to $\frac{\delta}{|b_1|}$; b_2 is the slope of the parameter or animals born in the genomic selection era (2013–2017), equal to $b_1 + \delta$.

²Slopes and SE are displayed in %. P -values and relative changes are not. F_{ROH} = inbreeding based on runs of homozygosity; ROH = runs of homozygosity; F_{HOM} = inbreeding based on excess homozygosity.

Table 8. Average rates of inbreeding (%) per year of birth (2000–2017) for Holsteins that have both pedigree and genomic information for the cows in the national herd (NatHerd) and genomic reference population (GInfo)¹

Parameter ²	Population	No. of animals 2000–2012	No. of animals 2013–2017	b_1 (\pm SE)	b_2 (\pm SE)	δ	P -value of δ	RC
F _{PED} subset (in %)	NatHerd	7,144	13,832	0.119 (\pm 0.006)	0.164 (\pm 0.014)	0.045	5.56e-237	0.38
	GInfo	12,379	17,601	0.092 (\pm 0.005)	0.141 (\pm 0.011)	0.049	7.38e-148	0.53
F _{ROH} regressed (in %)	NatHerd	7,144	13,832	0.227 (\pm 0.01)	0.359 (\pm 0.022)	0.133	0	0.58
	GInfo	12,379	17,601	0.179 (\pm 0.008)	0.288 (\pm 0.017)	0.108	0	0.60
F _{HOM} regressed (in %)	NatHerd	7,144	13,832	0.187 (\pm 0.013)	0.337 (\pm 0.024)	0.15	2.01e-195	0.80
	GInfo	12,379	17,601	0.201 (\pm 0.011)	0.129 (\pm 0.02)	-0.072	2.02e-48	0.36

¹ b_1 is the slope of regression of each parameter depending on birth year for animals born between 2000 and 2012 (pregenomics), and δ is the difference between the slopes of regression of each parameter depending on birth year for 2000–2012 and 2013–2017 (genomic selection) for animals in the national herd (NatHerd) and the genomic reference population (GInfo); the relative change (RC) is equal to $\frac{\delta}{|b_1|}$; b_2 is the slope of the parameter or animals born in the genomic selection era (2013–2017), equal to $b_1 + \delta$.

²Slopes and SE are displayed in %; P -values and relative changes are not. F_{PED} = inbreeding based on pedigree; F_{ROH} = inbreeding based on runs of homozygosity; F_{HOM} = inbreeding based on excess homozygosity.

by Doublet et al. (2019) for Holsteins, Montbéliarde, and Normande bulls for the French National Index (33, 50, and 71%, respectively). It should be noted that the BPI was introduced in 2016; for further details see Byrne et al. (2016), which replaced the Australian Profit Ranking (APR) index. Although both BPI and APR are multitrait selection indices, the BPI is arguably more popular than its predecessor. On top of this, DataGene was formed in 2016 with a view of bringing together pre-competitive herd improvement functions into a single entity (Newton et al., 2020). This may also have had a positive effect on the popularity and use of selection indices in Australia and could have contributed for the increase in rates of genetic gain in Australia.

One of the early expectations of GS was that increased rates of genetic gain in dairy cattle would largely be driven by a reduction in generation interval (Schaeffer, 2006). We observed a larger increase in genetic gain

for BPI in Holsteins compared with Jerseys where the decrease in sire age has been slower and only apparent in GInfo. The decrease in generation interval in the sire to breed cow pathway has been slower than observed in North America, where it was reported to be on average 5 yr in 2015 in US Holsteins (García-Ruiz et al., 2016) and 4 yr and 3.5 yr in 2017 in North American Holsteins and Jerseys, respectively (Makanjuola et al., 2020). This is possibly due to 2 factors: first, genomic selection was implemented in Australia in late 2011, 2 yr after it was released in the United States (VanRaden et al., 2009) and second, farmers have been slower to adopt GS through selecting younger (genomic) bulls, particularly in the Jersey breed, where the proportion of young bulls used under GS is similar to that of the progeny testing scheme.

The changes in genetic gain in Jerseys in the NatHerd is unlikely to be due to increased use of young bulls and is more likely to be driven by greater selection pressure

Table 9. Average rates of inbreeding (%) per year of birth (2000–2017) for Jerseys that have both pedigree and genomic information for the national herd (NatHerd) and genomic reference population (GInfo)¹

Parameter ²	Population	No. of animals 2000–2012	No. of animals 2013–2017	b_1 (\pm SE)	b_2 (\pm SE)	δ	P -value of δ	RC
F _{PED} subset (in %)	NatHerd	2,750	898	0.119 (\pm 0.018)	0.199 (\pm 0.06)	0.08	4.12e-30	0.67
	GInfo	2,027	2,697	0.031 (\pm 0.018)	0.079 (\pm 0.036)	0.048	1.15e-28	1.57
F _{ROH} regressed (in %)	NatHerd	2,750	898	0.294 (\pm 0.033)	0.611 (\pm 0.106)	0.318	1.01e-40	1.08
	GInfo	2,027	2,697	0.159 (\pm 0.035)	0.256 (\pm 0.061)	0.098	1.58e-68	0.62
F _{HOM} Regressed (in %)	NatHerd	2,750	898	0.303 (\pm 0.033)	0.658 (\pm 0.109)	0.355	1.04e-25	1.17
	GInfo	2,027	2,697	0.26 (\pm 0.037)	0.278 (\pm 0.063)	0.018	3.04e-35	0.07

¹ b_1 is the slope of regression of each parameter depending on birth year for animals born between 2000 and 2012 (pregenomics), and δ is the difference between the slopes of regression of each parameter depending on birth year for 2000–2012 and 2013–2017 (genomic selection) for animals in the national herd (NatHerd) and the genomic reference population (GInfo). The relative change (RC) is equal to $\frac{\delta}{|b_1|}$; b_2 is the slope of the parameter or animals born in the genomic selection era (2013–2017), equal to $b_1 + \delta$.

²Slopes and SE are displayed in %; P -values and relative changes are not. F_{PED} = inbreeding based on pedigree. F_{ROH} = inbreeding based on runs of homozygosity; F_{HOM} = inbreeding based on excess homozygosity.

in the selection of elite sires. Currently, the genetic gain for BPI in Jersey bulls under GS is lower than the pregenomic era, whereas in Holstein bulls it is increasing. One possible explanation is that Jersey breeders are not solely focused on the BPI. For example, we observed greater trends in cow EBV for stature, overall type, and mammary system (results not shown) than we observed for BPI.

The GS has also enhanced greater genetic gain for low heritability traits such as fertility. In Holstein cows, we observed negative rates of fertility before GS, then a largely positive shift in the fertility EBV under GS similar to the results presented in US Holsteins by García-Ruiz et al. (2016). In Holstein bulls, we found that the shift in fertility EBV occurred before the introduction of GS, possibly due to a shift in the importance of fertility in international selection indices and bull companies being concerned about the associated decline in fertility with increased milk yield. The prog-

ress in fertility may also be related to the availability of high fertility EBV bulls from overseas. A positive genetic trend in the fertility EBV is yet to be achieved in the Jersey cow populations, with the fertility EBV in the cow populations still declining but increasing moderately in bulls. This difference between Holstein and Jersey cow populations could be because Jersey breeders in Australia assume fertility of Jerseys is superior to Holsteins and do not see declining fertility as a priority. It should be noted that genetic evaluations are presented independently for Jerseys and Holsteins.

Differences in Genetic Diversity Between Glnfo Herds and National Herds

An important factor affecting the diversity of a population under GS is the diversity of an RP and whether it is representative of the population it is predicting (Pszczola and Calus, 2015). The results from this study

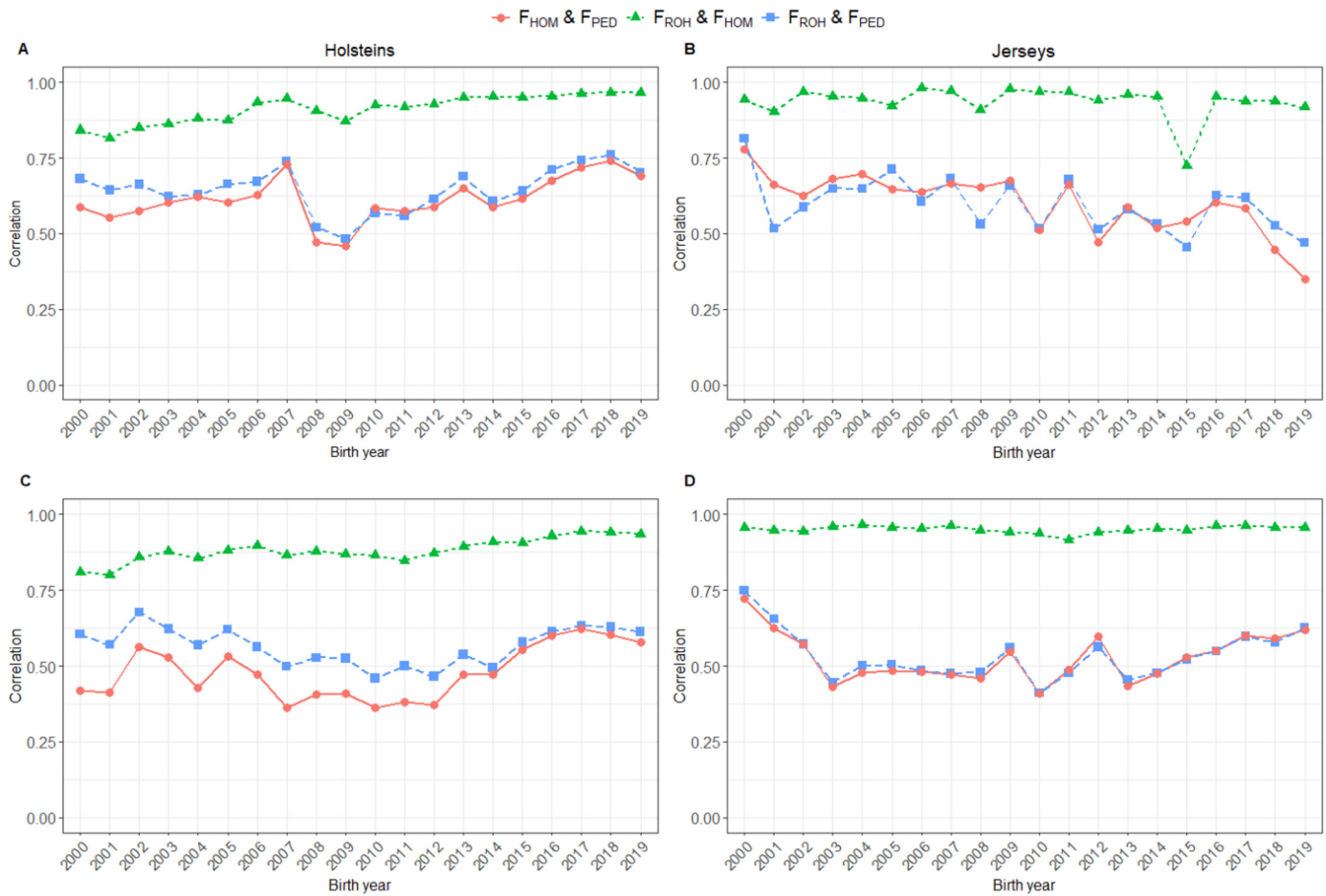


Figure 5. Correlations between difference in genome-wide estimates of inbreeding by year of birth for Holsteins (left) and Jerseys (right). A and B represent the correlations between bulls, and C and D represent the correlations between cows. F_PED = inbreeding based on pedigree; F_ROH = inbreeding based on runs of homozygosity; F_HOM = inbreeding based on excess homozygosity.

Table 10. Rate of genetic gain of Balanced Performance Index (BPI), protein EBV (Prot), and fertility EBV (Fert) per unit of increase in genomic inbreeding (F_{ROH}) for Holstein (HOL) and Jersey (JER) cows in the national herd (NatHerd), genomic reference (GInfo), and bull populations¹

Parameter	Breed	Population	b_1	b_2	δ	RC
BPI/ F_{ROH}	HOL	NatHerd	22.47	38.39	15.92	0.71
		GInfo	30.77	52.17	21.40	0.70
		Bulls	85.72	21.90	-63.82	-0.74
	JER	NatHerd	67.79	110.12	42.33	0.62
		GInfo	80.44	140.24	59.80	0.74
		Bulls	45.09	4.40	-40.69	-0.90
Prot/ F_{ROH}	HOL	NatHerd	3.52	3.08	-0.43	-0.12
		GInfo	4.21	2.80	-1.41	-0.33
		Bulls	4.70	1.15	-3.55	-0.76
	JER	NatHerd	6.94	13.21	6.27	0.90
		GInfo	7.66	12.05	4.39	0.57
		Bulls	2.84	-1.39	-4.22	-1.49
Fert/ F_{ROH}	HOL	NatHerd	-0.58	1.66	2.24	3.85
		GInfo	-0.78	2.57	3.35	4.28
		Bulls	2.33	0.51	-1.82	-0.78
	JER	NatHerd	-0.21	-1.61	-1.40	-6.82
		GInfo	-0.69	-0.35	0.34	0.49
		Bulls	-0.44	0.80	1.24	2.82

¹ b_1 is the slope of regression of each parameter depending on birth year for animals born between 2000 and 2012 (pregenomics); δ is the difference between the slopes of regression of each parameter depending on birth year for 2000–2012 and 2013–2017 (genomic selection) for animals in the national herd (NatHerd) or genomic reference population (GInfo); relative change (RC) is equal to $\frac{\delta}{|b_1|}$; b_2 is the slope of the parameter for animals born in the genomic selection era (2013–2017), equal to $b_1 + \delta$.

found that the within-herd relationships were greater than between-herd relationships. These findings are likely a result of sires of cows being more homogeneous within a herd. Jersey herds however had higher coancestry than Holsteins, both within and between herds, suggesting the use of less diverse bull teams or fewer bulls within a team. We found that on average Holstein breeders used around twice as many bulls compared with Jersey breeders (47 vs. 23 over the period between 2000 and 2017). A recent study by Makanjuola et al. (2020) demonstrated coancestry in a population (cows and bulls) of North American Holsteins and Jerseys to be 0.092 and 0.082, respectively, for the same year (2017). Although coancestry for Holsteins is in line with Makanjuola et al. (2020), the coancestry in Jerseys tends to be higher, though standard errors of the estimates are similar, which may be due to limited exchange of genetic material between Australia and other countries. High coancestry within Australian Jersey cattle populations may be the result of restricted availability of bulls through breeding companies and due to the small effective population size (Stachowicz et al., 2011; Makanjuola et al., 2020). Further work is required to determine if this high coancestry within the RP has an effect on the accuracy of GS for economic traits of outbred animals (Thomassen et al., 2020). Identifying and sourcing young high genetic merit bulls with low coancestry to the current RP and genotyping them can

improve genetic diversity and the accuracy of GS for outbred animals (Pszczola and Calus, 2015; Eynard et al., 2018).

Effect of GS on Inbreeding Levels in the Subpopulations

The introduction of GS has resulted in increases in both the rate of inbreeding and average inbreeding levels in all Holstein and Jersey subpopulations. In this study, we used a regression to determine the inbreeding rates, which was the same framework used for breeding values and is consistent with Doublet et al. (2019) and Pryce et al. (2014). This approach is different from that used by Falconer and Mackay (1996) where the inbreeding rate is calculated as

$$\Delta F = \frac{F(t) - F(t-1)}{1 - F(t-1)},$$

where ΔF is the rate of inbreeding, $F(t)$ is the average inbreeding level at a given year, and t is time in years ranging from 2000 to 2017. In Holsteins, our results showed little to no difference between the method used in this study versus the one used in population genetics (difference in F_{PED} : 0 to 0.06; difference in F_{ROH} : -0.06 to 0.18; Supplemental Table S1, <https://doi.org/>

10.6084/m9.figshare.15153495.v2). There were larger differences in the Jersey population (difference in F_{PED} : 0.01 to 0.08; difference in F_{ROH} : -0.05 to 0.23; Supplemental Table S2, <https://doi.org/10.6084/m9.figshare.15153495.v2>). As a result, caution needs to be taken when comparing the rates of inbreeding in Jerseys to other studies.

The same issue is likely to be true for F_{HOM} . The Jersey population was smaller than the Holstein population and so the population allele frequency is likely to be most accurately estimated in the GInfo Holstein population. This means that F_{HOM} is likely to be most robust in GInfo Holsteins. Again, this is a strength of having a dedicated female RP such as GInfo, where most animals in the herds participating in the scheme are routinely genotyped. As NatHerd is likely to have preferential genotyping strategy, there is a risk that the allele frequencies may be biased.

In comparison to previous studies, Holstein bulls in this study had a lower rate of pedigree-based inbreeding in the pregenomics period (0.08–0.15%), whereas ΔF_{PED} in the post-GS period was more than 2 times higher (0.34–0.55%; Doekes et al., 2018; Doublet et al., 2019; Makanjuola et al., 2020). The depth of pedigree and a greater bull diversity used for artificial breeding potentially explains the observed difference pre-GS between Australia and elsewhere. When using F_{ROH} to estimate inbreeding, the rate of inbreeding pre-GS is greater than those found by others (Doekes et al., 2018; Doublet et al., 2019; CDCB, 2020; Makanjuola et al., 2020; 0.08–0.16%). After the introduction of GS, the rate of inbreeding is higher than reported in the Netherlands, France, and North America (Doekes et al., 2018; Doublet et al., 2019; CDCB, 2020; Makanjuola et al., 2020). Additionally, the average length of an ROH increased 50 kb under GS, whereas Doublet et al. (2019) observed an increase of only 13 kb. One possible explanation for these differences post-GS could be the duration over which the study was conducted. In the current study, we used data until 2017, whereas Doekes et al. (2018) and Doublet et al. (2019) data were only until 2015. When using comparable years, we observe a similar ΔF to those of Doekes et al. (2018) and Doublet et al. (2019).

Few studies have investigated the effect of GS on inbreeding in Jerseys. Makanjuola et al. (2020) used a population of cows and bulls over a similar period and observed a decline in the ΔF_{PED} and ΔF_{ROH} (-0.5 and -0.08%, respectively) in the pre-GS period and an increase of 0.18% in the post-GS period. The results of our pedigree inbreeding are in line with reported results elsewhere (CDCB, 2020; Makanjuola et al., 2020); however, when using F_{ROH} it is almost twice as

high. Pedigree inbreeding values are likely to be underestimated in this study due to less complete pedigrees (96.2 vs. 98.8%), which is known to affect pedigree inbreeding coefficients (Cassell et al., 2003). The higher F_{ROH} values are probably due to different subpopulations being used, this study analyzed the cows and bulls separately and observed differences between the 2, whereas Makanjuola et al. (2020) analyzed them together. Further, the small sample size of both Jersey cows and bulls may also have affected the result in the current study. Caution should be made when interpreting inbreeding values from the NatHerd, as there is likely a sampling bias.

The high level of inbreeding in both the Holstein and Jersey bull populations has yet to be reflected extensively in the cow population. The rate and average values of inbreeding and genetic gain are slower in cows compared with bulls which could be explained by genetic lag (Dechow et al., 2018) and depth of pedigree. Cows in this study had less complete pedigrees and in general, have a lower selection intensity and greater diversity compared with bulls used in artificial insemination.

When making inbreeding comparisons between the 2 cow populations GInfo herds had higher F_{PED} and a greater ΔF_{PED} than the NatHerd. Greater rates of pedigree and genomic inbreeding were also observed in a subset of animals with genotype data, suggesting actual inbreeding levels could be higher in the national population but is poorly estimated. In Holsteins, cows in the NatHerd had larger increases in F_{ROH} and F_{HOM} compared with what we observed in F_{PED} . Similar trends were observed in Jerseys where the NatHerd had the greatest changes in F_{ROH} and F_{HOM} after GS (Table 9). This could partly be an artifact of having more complete pedigrees and earlier adoption of GS in young bulls, respectively. However, could also be due to selective genotyping of elite females. Further work is required to determine the proportion of animals genotyped within a herd-year for the NatHerd in both breeds. Knowing the magnitude of inbreeding in Australian dairy herds is challenging as detailed pedigree records are limited and only a small proportion of cows are genotyped (Ooi et al., 2021).

Genetic Gain Per Unit of Inbreeding

The rate of inbreeding has increased after the introduction of GS and the increased rates of genetic gain are expected to outweigh the losses caused by inbreeding depression. Conversely, the more inbreeding depression at a trait, a lower genetic gain can be expected. For example, the protein EBV has increased by 4.4

kg under GS (over 5 yr; 2013–2017) in GInfo Holstein cows, whereas F_{ROH} has increased by 1.15%. Inbreeding was estimated to be associated with a reduction of 0.63 kg protein per 1% increase in inbreeding (Pryce et al., 2014) therefore after correcting for inbreeding depression, our net gain is likely to be reduced to 3.6 kg of protein.

We observed increases in genetic gain per unit of inbreeding in cows but large decreases in bulls. These findings in bulls are consistent with Doublet et al. (2019), who observed decreases in the French index (ISU) Holstein and Normande bulls (88 to 21 ISU/ F_{ROH} and 58 to 31 ISU/ F_{ROH} , respectively). Interestingly, they observed an increase in Montbéliarde bulls from 36 to 44 ISU/ F_{ROH} . For individual traits, we observed varied responses. In Holstein cows, we observed similar gains per unit of inbreeding for protein yield and increases in the fertility EBV, whereas in Holstein bulls, we observed decreases after GS was introduced. These findings are consistent with García-Ruiz et al. (2016), who found similar decreases in US Holsteins in traits of moderate heritability and increases in traits of low heritability in Holstein cows. In Jerseys, cows in the NatHerd increased in protein yield, whereas GInfo remained similar. Fertility in both Jersey cow populations remained negative per unit of inbreeding however increases were observed in Jersey bulls. Further validation is required however this method could provide guidance for indices and traits that are rapidly losing diversity which is not offset by an increase in genetic gain.

In the current study, in the postgenomic era, the rate of inbreeding has been increasing at a faster rate than the pregenomic era. The rate of increase in some of the subpopulations (Supplemental Tables S1 and S2, <https://doi.org/10.6084/m9.figshare.15153495.v2>) is higher than the 1% per generation increased recommended (FAO, 2015). Constraining inbreeding to an acceptable level requires measures at both the population and herd level. At a population level, one approach is penalizing a bull's index of overall genetic merit based on its coancestry with the national herd (e.g., the United States; Sun et al., 2014). A similar approach was proposed by Pryce et al. (2012) and used a weighting on the pedigree or genomic coancestry between candidate mates to penalize the parent average Australian selection index. This approach has not yet been implemented. Our results clearly show that introducing ways to monitor and control inbreeding should be a priority for the Australian dairy industry. An approach to reduce inbreeding at a herd level is already happening and several breeding companies are developing mating programs that include genomic information and genomic

inbreeding measures and these could help to reduce the negative effect inbreeding in the short term. Therefore, it is important to ensure that research approaches can be integrated through to the herd level for the collective management of inbreeding.

CONCLUSIONS

Genomic selection has increased genetic gain and reduced genetic diversity in both cows and bulls in Australia. On the other hand, genetic gain in Jersey herds has been lower than expected, which could partly be due to the slower uptake of young genomic bulls and the smaller size of the Jersey population. Overall, greater genetic gain and reduction in diversity over time were faster in bulls followed by the cows in the GInfo herd than the non-GInfo national herd as expected. The lag in genetic gain between bulls and cows appears to be wider in Jerseys than Holsteins and more so for low heritability traits (such as fertility) than for a medium heritability trait (protein) and BPI (the economic index). The measures of inbreeding used here along with the availability of a good genomic RP herd will be useful to infer and track future differences in genetic gain and diversity of the national herds.

ACKNOWLEDGMENTS

This study was supported by DairyBio (Melbourne, Australia), funded by Dairy Australia (Melbourne, Australia), the Gardiner Foundation (Melbourne, Australia), and Agriculture Victoria (Melbourne, Australia). The authors thank DataGene Ltd. and their staff for the provision of both phenotype and genotype data. The authors also thank Christy van der Jagt and Iona MacLeod (Agriculture Research Victoria, Melbourne, Australia) for useful conversations that have helped in the development of this paper. The authors have not stated any conflicts of interest.

REFERENCES

- Aggarwal, C. C. 2013. Probabilistic and statistical models for outlier detection. Pages 41–74 in *Outlier Analysis*. Springer International Publishing. https://doi.org/10.1007/978-1-4614-6396-2_2.
- Alexander, D. H., J. Novembre, and K. Lange. 2009. Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* 19:1655–1664. <https://doi.org/10.1101/gr.094052.109>.
- Bjelland, D. W., K. A. Weigel, N. Vukasinovic, and J. D. Nkrumah. 2013. Evaluation of inbreeding depression in Holstein cattle using whole-genome SNP markers and alternative measures of genomic inbreeding. *J. Dairy Sci.* 96:4697–4706. <https://doi.org/10.3168/jds.2012-6435>.
- Boichard, D. 2002. PEDIG: A Fortran Package for Pedigree Analysis Suited for Large Populations. Proc. 7th World Congress on Genetics Applied to Livestock Production, Session 28.

- Byrne, T. J., B. F. S. Santos, P. R. Amer, D. Martin-Collado, J. E. Pryce, and M. Axford. 2016. New breeding objectives and selection indices for the Australian dairy industry. *J. Dairy Sci.* 99:8146–8167. <https://doi.org/10.3168/jds.2015-10747>.
- Calus, M. P. L., Y. de Haas, and R. F. Veerkamp. 2013. Combining cow and bull reference populations to increase accuracy of genomic prediction and genome-wide association studies. *J. Dairy Sci.* 96:6703–6715. <https://doi.org/10.3168/jds.2012-6013>.
- Cassell, B. G., V. Adamec, and R. E. Pearson. 2003. Effect of incomplete pedigrees on estimates of inbreeding and inbreeding depression for days to first service and summit milk yield in Holsteins and Jerseys. *J. Dairy Sci.* 86:2967–2976. [https://doi.org/10.3168/jds.S0022-0302\(03\)73894-6](https://doi.org/10.3168/jds.S0022-0302(03)73894-6).
- CDCB (Council on Dairy Cattle Breeding). 2020. Inbreeding trends available from CDCB. Accessed June 2020. <https://queries.uscdcb.com/eval/summary/inbrd.cfm>.
- Dassonneville, R., A. Baur, S. Fritz, D. Boichard, and V. Ducrocq. 2012. Inclusion of cow records in genomic evaluations and impact on bias due to preferential treatment. *Genet. Sel. Evol.* 44:40. <https://doi.org/10.1186/1297-9686-44-40>.
- de Roos, A. P. W., C. Schrooten, R. F. Veerkamp, and J. A. M. van Arendonk. 2011. Effects of genomic selection on genetic improvement, inbreeding, and merit of young versus proven bulls. *J. Dairy Sci.* 94:1559–1567. <https://doi.org/10.3168/jds.2010-3354>.
- Dechow, C. D., W. S. Liu, J. S. Idun, and B. Maness. 2018. Short communication: Two dominant paternal lineages for North American Jersey artificial insemination sires. *J. Dairy Sci.* 101:2281–2284. <https://doi.org/10.3168/jds.2017-13694>.
- Doekes, H. P., R. F. Veerkamp, P. Bijma, S. J. Hiemstra, and J. J. Windig. 2018. Trends in genome-wide and region-specific genetic diversity in the Dutch-Flemish Holstein-Friesian breeding program from 1986 to 2015. *Genet. Sel. Evol.* 50:15.
- Doublet, A.-C., P. Croiseau, S. Fritz, A. Michenet, C. Hozé, C. Danchin-Burge, D. Laloë, and G. Restoux. 2019. The impact of genomic selection on genetic diversity and genetic gain in three French dairy cattle breeds. *Genet. Sel. Evol.* 51:52. <https://doi.org/10.1186/s12711-019-0495-1>.
- Eynard, S. E., P. Croiseau, D. Laloë, S. Fritz, M. P. L. Calus, and G. Restoux. 2018. Which individuals to choose to update the reference population? Minimizing the loss of genetic diversity in animal genomic selection programs. *G3* 8:113–121.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to Quantitative Genetics*. 4th ed. Longman.
- FAO (Food and Agriculture Organization of the United Nations). 2015. *The Second Report on the State of the World's Animal Genetic Resources for Food and Agriculture*. B. D. Scherf and D. Pilling, ed. FAO Commission on Genetic Resources for Food and Agriculture Assessments.
- Forutan, M., S. Ansari Mahyari, C. Baes, N. Melzer, F. S. Schenkel, and M. Sargolzaei. 2018. Inbreeding and runs of homozygosity before and after genomic selection in North American Holstein cattle. *BMC Genomics* 19:98. <https://doi.org/10.1186/s12864-018-4453-z>.
- García-Ruiz, A., J. B. Cole, P. M. VanRaden, G. R. Wiggins, F. J. Ruiz-López, and C. P. Van Tassell. 2016. Changes in genetic selection differentials and generation intervals in US Holstein dairy cattle as a result of genomic selection. *Proc. Natl. Acad. Sci. USA* 113:E3995–E4004. <https://doi.org/10.1073/pnas.1519061113>.
- Goddard, M. 2009. Genomic selection: Prediction of accuracy and maximisation of long term response. *Genetica* 136:245–257. <https://doi.org/10.1007/s10709-008-9308-0>.
- González-Recio, O., E. Lopez de Maturana, and J. P. Gutierrez. 2007. Inbreeding depression on female fertility and calving ease in Spanish dairy cattle. *J. Dairy Sci.* 90:5744–5752. <https://doi.org/10.3168/jds.2007-0203>.
- 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. <https://doi.org/10.1017/S0016672398003474>.
- Hayes, B. J., P. J. Bowman, A. J. Chamberlain, and M. E. Goddard. 2009. Invited review: Genomic selection in dairy cattle: Progress and challenges. *J. Dairy Sci.* 92:433–443. <https://doi.org/10.3168/jds.2008-1646>.
- Heffner, E. L., A. J. Lorenz, J.-L. Jannink, and M. E. Sorrells. 2010. Plant breeding with genomic selection: Gain per unit time and cost. *Crop Sci.* 50:1681–1690. <https://doi.org/10.2135/cropsci2009.11.0662>.
- Howard, J. T., J. E. Pryce, C. Baes, and C. Maltecca. 2017. Invited review: Inbreeding in the genomics era: Inbreeding, inbreeding depression, and management of genomic variability. *J. Dairy Sci.* 100:6009–6024. <https://doi.org/10.3168/jds.2017-12787>.
- Lencz, T., C. Lambert, P. DeRosse, K. E. Burdick, T. V. Morgan, J. M. Kane, R. Kucherlapati, and A. K. Malhotra. 2007. Runs of homozygosity reveal highly penetrant recessive loci in schizophrenia. *Proc. Natl. Acad. Sci. USA* 104:19942–19947. <https://doi.org/10.1073/pnas.0710021104>.
- Maignel, L., D. Boichard, and E. Verrier. 1996. Genetic variability of French dairy breeds estimated from pedigree information. *Interbull Bull.* 14:49–56.
- Makanjuola, B. O., F. Miglior, E. A. Abdalla, C. Maltecca, F. S. Schenkel, and C. F. Baes. 2020. Effect of genomic selection on rate of inbreeding and coancestry and effective population size of Holstein and Jersey cattle populations. *J. Dairy Sci.* 103:5183–5199. <https://doi.org/10.3168/jds.2019-18013>.
- Mc Parland, S., J. F. Kearney, M. Rath, and D. P. Berry. 2007. Inbreeding effects on milk production, calving performance, fertility, and conformation in Irish Holstein-Friesians. *J. Dairy Sci.* 90:4411–4419. <https://doi.org/10.3168/jds.2007-0227>.
- Meuwissen, T. H. E. 1997. Maximizing the response of selection with a predefined rate of inbreeding. *J. Anim. Sci.* 75:934–940. <https://doi.org/10.2527/1997.754934x>.
- Meuwissen, T. H. E., B. J. Hayes, and M. E. Goddard. 2001. Prediction of total genetic value using genome-wide dense marker maps. *Genetics* 157:1819–1829. <https://doi.org/10.1093/genetics/157.4.1819>.
- Newton, J. E., R. Nettle, and J. E. Pryce. 2020. Farming smarter with big data: Insights from the case of Australia's national dairy herd milk recording scheme. *Agric. Syst.* 181:102811. <https://doi.org/10.1016/j.agsy.2020.102811>.
- Nieuwhof, G., K. Beard, K. Konstantinov, P. Bowman, and B. Hayes. 2010. Implementation of genomics in Australia. *Interbull Bull.* 42:35–39.
- Ooi, E., M. A. Stevenson, D. S. Beggs, P. D. Mansell, J. E. Pryce, A. Murray, and M. F. Pyman. 2021. Herd manager attitudes and intentions regarding the selection of high-fertility EBV sires in Australia. *J. Dairy Sci.* 104:4375–4389. <https://doi.org/10.3168/jds.2020-18552>.
- Pryce, J. E., M. Haile-Mariam, M. E. Goddard, and B. J. Hayes. 2014. Identification of genomic regions associated with inbreeding depression in Holstein and Jersey dairy cattle. *Genet. Sel. Evol.* 46:71. <https://doi.org/10.1186/s12711-014-0071-7>.
- Pryce, J. E., B. J. Hayes, and M. E. Goddard. 2012. Genotyping dairy females can improve the reliability of genomic selection for young bulls and heifers and provide farmers with new management tools in Proc. of ICAR 38th Biennial Meeting, International Committee for Animal Recording (ICAR), Cork, Ireland.
- Pryce, J. E., T. T. Nguyen, M. Axford, G. Nieuwhof, and M. Shaffer. 2018. Symposium review: Building a better cow—The Australian experience and future perspectives. *J. Dairy Sci.* 101:3702–3713. <https://doi.org/10.3168/jds.2017-13377>.
- Pszczola, M., and M. P. L. Calus. 2015. Updating the reference population to achieve constant genomic prediction reliability across generations. *Animal* 10:1018–1024.
- Purcell, S., B. Neale, K. Todd-Brown, L. Thomas, M. A. R. Ferreira, D. Bender, J. Maller, P. Sklar, P. I. W. de Bakker, M. J. Daly, and P. C. Sham. 2007. PLINK: A tool set for whole-genome association and population-based linkage analyses. *Am. J. Hum. Genet.* 81:559–575. <https://doi.org/10.1086/519795>.
- Schaeffer, L. 2006. Strategy for applying genome-wide selection in dairy cattle. *J. Anim. Breed. Genet.* 123:218–223. <https://doi.org/10.1111/j.1439-0388.2006.00595.x>.

- Schütz, E., M. Scharfenstein, and B. Brenig. 2008. Implication of complex vertebral malformation and bovine leukocyte adhesion deficiency DNA-based testing on disease frequency in the Holstein population. *J. Dairy Sci.* 91:4854–4859. <https://doi.org/10.3168/jds.2008-1154>.
- Stachowicz, K., M. Sargolzaei, F. Miglior, and F. S. Schenkel. 2011. Rates of inbreeding and genetic diversity in Canadian Holstein and Jersey cattle. *J. Dairy Sci.* 94:5160–5175. <https://doi.org/10.3168/jds.2010-3308>.
- Sun, C., P. M. VanRaden, J. B. Cole, and J. R. O'Connell. 2014. Improvement of prediction ability for genomic selection of dairy cattle by including dominance effects. *PLoS One* 9:e103934. <https://doi.org/10.1371/journal.pone.0103934>.
- Thomassen, J. R., H. Liu, and A. C. Sørensen. 2020. Genotyping more cows increases genetic gain and reduces rate of true inbreeding in a dairy cattle breeding scheme using female reproductive technologies. *J. Dairy Sci.* 103:597–606. <https://doi.org/10.3168/jds.2019-16974>.
- Thompson, E. A. 2013. Identity by descent: Variation in meiosis, across genomes, and in populations. *Genetics* 194:301–326. <https://doi.org/10.1534/genetics.112.148825>.
- VanRaden, P. M. 1992. Accounting for inbreeding and crossbreeding in genetic evaluation of large populations. *J. Dairy Sci.* 75:3136–3144. [https://doi.org/10.3168/jds.S0022-0302\(92\)78077-1](https://doi.org/10.3168/jds.S0022-0302(92)78077-1).
- VanRaden, P. M. 2008. Efficient methods to compute genomic predictions. *J. Dairy Sci.* 91:4414–4423. <https://doi.org/10.3168/jds.2007-0980>.
- VanRaden, P. M., C. P. Van Tassell, G. R. Wiggans, T. S. Sonstegard, R. D. Schnabel, J. F. Taylor, and F. S. Schenkel. 2009. Invited review: Reliability of genomic predictions for North American Holstein bulls. *J. Dairy Sci.* 92:16–24. <https://doi.org/10.3168/jds.2008-1514>.
- Woolliams, J. A., P. Berg, B. S. Dagnachew, and T. H. E. Meuwissen. 2015. Genetic contributions and their optimization. *J. Anim. Breed. Genet.* 132:89–99. <https://doi.org/10.1111/jbg.12148>.

ORCID

- B. A. Scott  <https://orcid.org/0000-0002-8737-6320>
M. Haile-Mariam  <https://orcid.org/0000-0001-5476-7475>
B. G. Cocks  <https://orcid.org/0000-0001-9776-1508>
J. E. Pryce  <https://orcid.org/0000-0002-1397-1282>