Temporal trends in estimated breeding values for daughter fertility in Holstein and Jersey cows in the Australian dairy industry

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Handling Editor:
Sue Hatcher

ABSTRACT

Context. Milk yield and fertility are negatively genetically correlated in dairy cows, so selection for milk yield would be expected to result in genetic deterioration in fertility unless there is concurrent selection for fertility. **Aim.** The main study aim was to describe temporal trends in estimated breeding values (Australian Breeding Values, ABVs) for daughter fertility for Holstein and Jersey cows in Australian dairy herds. **Methods.** A retrospective descriptive study was conducted using milk recording and ABV data from cows in commercial dairy herds. Calvings and lactations from 1980 to 2022 were used, along with ABVs for cows that calved over that period and for sires of those cows. Herd-year mean estimated breeding values were calculated for each breed as the means for cows of that breed that calved in the herd that year. **Key results.** Daughter fertility ABVs declined (i.e. deteriorated) markedly in Holsteins in the Australian dairy industry, commencing before 1980. Rates of decline were most rapid in sires, less rapid in cows and least rapid at herd level. Selection pressure for cows with higher daughter fertility ABVs due to cow culling decisions was probably occurring within Australian herds but any such effect was minimal. The decline in cow daughter fertility ABVs is being reversed, but recovery of herd means in the study population has been slow. The rate of decline in daughter fertility ABVs in Jersey cows was less than for Holsteins. **Conclusions.** Over a period of genetic deterioration, then recovery for a trait, genetic trends in sires are not closely related to genetic trends at herd level. The rapid decline in daughter fertility ABVs for sires probably resulted in substantial reductions in herd reproductive performance and cow longevity in Holstein herds in the Australian dairy industry. Under current trends, it will be a considerable time before the adverse effects of the decline in daughter fertility ABVs are fully reversed. **Implications.** An important ongoing task for animal breeding is to identify and monitor traits that may become important for farmers and community in future but may be declining genetically under current selection decisions.

Keywords: Australian Breeding Values, dairy cows, daughter fertility, fertility, genetics, Holsteins, Jerseys, reproductive performance, temporal trends.

Introduction

Herd reproductive performance is an important determinant of herd profit, management simplicity and diversity of management options in dairy herds. Herd reproductive performance is multi-factorial, and is partly determined by the cows' true breeding values for daughter fertility. At cow level, there is only a weak negative phenotypic relationship between milk yield and reproductive performance (Rearte *et al.* 2018). However, as milk production and fertility are negatively genetically correlated (VanRaden *et al.* 2004), selection for milk production without concurrent selection for fertility would be expected to result in a deterioration in breeding values for fertility, and deteriorations in breeding values for fertility have been reported in numerous countries (Pryce *et al.* 2014) concurrent with genetic increases in milk production traits.

As the purpose of genetic improvement is to increase herd profitability, it is important that genetic trends are described at herd level. Genetic trends have been reported as unweighted means for sires by the sires' years of birth (Ma *et al.* 2019; Guinan *et al.* 2023), but these would not be expected to closely reflect genetic trends in females at the herd level. This is because numbers of daughters reaching first calving will vary by sire, being determined collectively by herd-manager sire-selection decisions, the proportion of each sire's inseminations where sexed semen is used, differences in conception rates, pregnancy and perinatal loss by sire, and herd-manager heifer-retention decisions. Further, the genetic merit of cows by year of birth will depend not only on the genetic merit of the cows' sire, but also on the genetic merit of the cows' dam, the latter depending not only on genetic merit of sires weighted by numbers of daughter of each sire that reach first calving but also on the longevity of cows of various genetic merit in the herd. Accordingly, some workers have also reported means for cows by cow's year of birth (Ma *et al.* 2019). However, the genetic mean for a lactating herd in any particular year is determined by the genetic merit of cows that calve in that year. This, in turn, depends collectively on the genetic merit of cows by their year of birth, the proportion of female calves born that calve and enter the herd, and the longevity of cows of various genetic merit. Given this complexity, to understand herd-level impacts of genetic trends among sires, there is a need to describe genetic trends for cows by cow's year of birth and for herds by year using cows that calved in that year. Impacts of herd-level genetic changes in fertility can then be inferred using estimated effects of cow fertility breeding value on reproductive performance at lactation level.

In commercial dairy herds, it is plausible that deteriorations in genetic merit for fertility among sires are partly counteracted by positive selection pressure for genetic merit for fertility due to cow culling and retention decisions. Cows with greater genetic merit for fertility would be more likely to produce herd-replacement heifers than would cows with lower genetic merit for fertility if the former have increased longevity. This is plausible as herd managers cull non-conceiving cows and preferentially retain cows that conceive more rapidly. In addition, in many seasonal and split calving herds, the herd's replacement heifers are chosen from the progeny of the earliest conceiving cows, a further selection pressure favouring cows with greater genetic merit for fertility. Thus, it was of interest to assess the likely magnitude of selection pressure for genetic merit for fertility due to cow culling decisions.

The aims of this study were to describe temporal trends in Australian Breeding Values (ABVs) for daughter fertility for sires by sire's year of birth, for cows, cows' sires and dams by cow's year of birth, and for herds by year (means for all cows that calved by year of calving) for Holstein and Jersey cows in Australian dairy herds, and to investigate the likely magnitude of selection pressures for genetic merit for fertility due to cow culling decisions.

Materials and methods

A retrospective descriptive study was conducted using milk recording data from commercial dairy herds that had been aggregated by DataGene, manager of Australia's central data repository for such data. All calvings and lactations from 1980 were used, along with ABVs for cows that calved over that period and for sires and dams of those cows. ABVs had been calculated by DataGene on 9 August 2022. These had been calculated using the best linear unbiased prediction of Henderson (1953) for numerous production, health and management traits, including daughter fertility, with blending used to combine pedigree, herd recording and genomic information (Nieuwhof *et al.* 2010). Data were exported from the central data repository on 15 November 2022.

Breeds of cows were identified using four-character breed codes as entered by the herd managers in conjunction with the sire breed codes determined centrally and used for genetic analyses. Cows whose four-character breed code was 'FFFF' and sire breed code was 'F' were selected for analyses as Holsteins and cows whose four-character breed code was 'JJJJ' and sire breed code was 'J' were selected for analyses as Jerseys. The four-character breed code consists of characters indicating the breed of, in sequence from left to right, the animal's paternal grandfather, paternal grandmother, maternal grandfather and maternal grandmother. For cows, the sire breed code indicates the breed under which the cows' ABVs were calculated.

Separately within Holsteins and Jerseys, mean sire ABVs were calculated by sire year of birth, mean cow ABVs, cows' sire ABVs and cows' dam ABVs were calculated for all cows by cow's year of birth, and mean cow ABVs were calculated for all calvings by year of calving. Only sires with at least one daughter calved in a study herd and only cows that calved at least once in a study herd were included in analyses.

Mean cows' daughter fertility ABVs were also calculated for calvings by Holstein cows by cow age at calving (2–12 years) by year of calving. Cow ages at calving in years were calculated as ages in days rounded to the nearest integer.

To assess effects of cow culling decisions on mean cow daughter fertility ABVs for cows still in study herds at various ages, the following eight birth cohorts were identified: cows born in each of 1980, 1985, 1990, 1995, 2000, 2005, 2010 and 2015. Only Holstein cows that calved as 2-year olds in herds with calvings in the dataset for that and the next 10 years were included in these analyses. Within each birth cohort, mean cow daughter fertility ABV was calculated for each age category.

Herd-year mean ABVs were also calculated for Holstein cows as the means of ABVs for cows that calved in the herd

in that year. Herd-year mean ABVs were used only for herd-years with at least 100 calvings by cows of that breed and where between 6% and 29% of those cows were aged <30 months, and between 29% and 54% were aged ≥60 months at that calving. These age restrictions were applied to ensure that herd-years with extreme atypical cow age distributions (such as herd-years where most calvings were by 2- and 3-year old cows) were not selected. These cutpoints were the 10th and 90th percentile values for all herd-years from 1980 with at least 100 calvings.

Results

Numbers of calvings and lactations, cows, sires and herds

Data were available for 33 016 089 calvings and lactations from 1980 to 2022 by 10 930 451 cows in 27 965 herds. Of these 10 930 451 cows, breed data were available for 70% (7 695 329), including 4 921 099 Holstein cows and 875 240 Jersey cows. Sire was recorded for 93% (4 600 295) and 94% (821 236) of these Holstein and Jersey cows respectively. Numbers of sires with at least one daughter calved in a study herd on or between 1980 and 2022 by sire's year of birth are shown in Supplementary material Table S1, along with distributions of numbers of these daughters per sire. Most sires had few daughters but a small proportion of sires had very large numbers of daughters.

The cow's ABVs for daughter fertility were available for 78% (3 830 725) of Holstein cows and 82% (714 595) of Jersey cows. The cow's sire and dam ABVs for daughter fertility were available respectively, for 93% and 60% of Holstein cows, and 91% and 59% of Jersey cows. Numbers of cows by cow's year of birth are shown in Table S2.

Of the 33 016 089 calvings, breed data for the associated cow were available for 26 521 392 (80%), including 16 796 920 calvings by Holstein cows and 3 141 838 calvings by Jersey cows. ABVs for daughter fertility were available for the cow for 88% (14 800 049) of calvings by Holstein cows and 90% (2 839 999) of calvings by Jersey cows. Numbers of calvings and numbers of herds by year (herd-years) within breed are shown in Table S3.

Mean daughter fertility ABVs pooled

Mean daughter fertility ABVs for sires by sire's year of birth are shown in Fig. 1. Higher values of the daughter fertility ABVs result in better reproductive performance from genetic effects (i.e. shorter times to conception; Morton *et al.* 2017; Ooi *et al.* 2022). For Holstein sires, mean daughter fertility ABVs declined for sires born from 1980 to 2009, with steepest decline occurring from 1980 to 2000, and increasing rapidly for sires born from 2010. The rate of increase from 2010 was considerably greater than the rate of decline from 1980 to 2000. For Jersey sires, mean daughter fertility ABVs decreased from 1980 to 2016.

Mean daughter fertility ABVs for cows, cows' sires and cows' dams by cow's year of birth for Holstein cows are
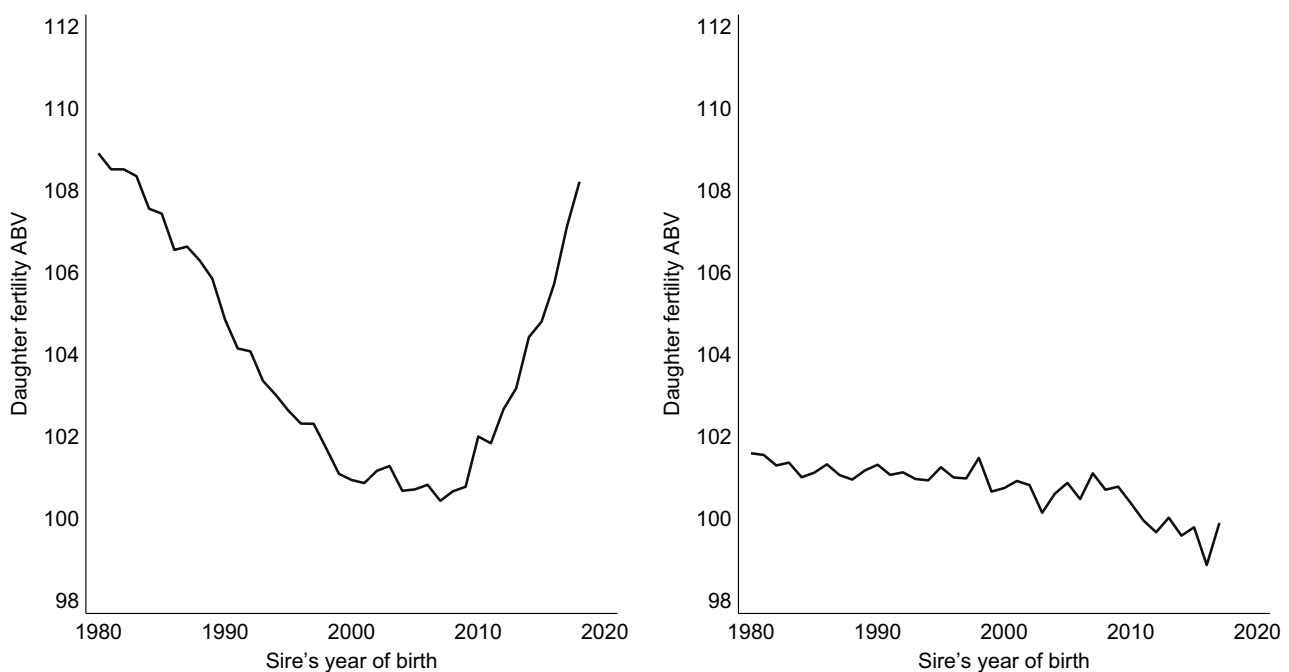

Fig. 1. Mean daughter fertility ABVs for sires with at least one daughter calved in a study herd by sire's year of birth for Holstein sires (left-hand side) and Jersey sires (right-hand side). Means are shown only for years of birth with at least 73 sires of the respective breed.
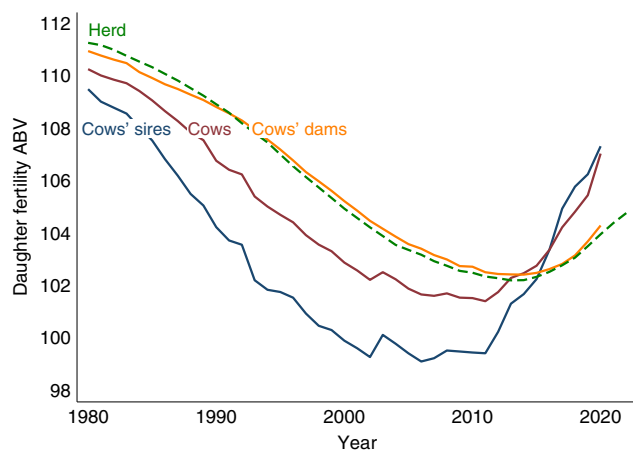
Fig. 2. Mean daughter fertility ABVs for Holstein cows, cows' sires and cows' dams by cow's year of birth, and mean cow daughter fertility ABVs for all calvings by Holstein cows by year of calving ('Herd'; dashed line).

Fig. 3. Mean daughter fertility ABVs for Jersey cows, cows' sires and cows' dams by cow's year of birth, and mean cow daughter fertility ABVs for all calvings by Jersey cows by year of calving ('Herd'; dashed line).

shown in Fig. 2. 'Herd' means were also plotted, calculated as mean cow daughter fertility ABVs for all calvings in the year by year of calving. Each of these can be considered as estimating the national 'herd' mean where all calvings in the year are considered as constituting a single 'herd'. Genetic trends for sires by sire's year of birth were not closely related to genetic trends at herd level. From 2010, means for cows' sires by cow's year of birth (Fig. 2) were less than, but increased at a similar rate to, the means for all sires by sire's year of birth (Fig. 1, Supplementary Fig. S1), consistent with lags of 2–3 years between sires' and daughters' birth dates. However, from 1990 to 2010, means for cows' sires did not reflect means for all sires lagged by 2–3 years. Instead, over this period, means for cows' sires were less than means for all sires, even though means for both groups declined markedly from 1990 to 2000. Mean daughter fertility ABVs for cows' sires declined markedly from just under 110 for sires of the cows born in 1980 before generally reaching a plateau from 2002 and then increasing rapidly and approximately linearly for sires of the cows born from 2011 to 2020 (Fig. 2). Mean daughter fertility ABVs for cows' dams also declined considerably, but less rapidly, than for cows' sires until 2013, before increasing, also less rapidly than for cows' sires. Mean daughter fertility ABVs for cows declined markedly to 101 for cows born in 2011, then increased rapidly for subsequent birth cohorts. Mean daughter fertility ABVs for cows' dams declined less rapidly than means for cows until 1992. National herd means of cow daughter fertility ABVs declined from 111 for calvings in 1980 to 102 for calvings in 2013, before increasing to 105 for calvings in 2022. Results were similar when only cows with daughter fertility ABVs available for all three of the cow, her sire and her dam were included (results not shown).
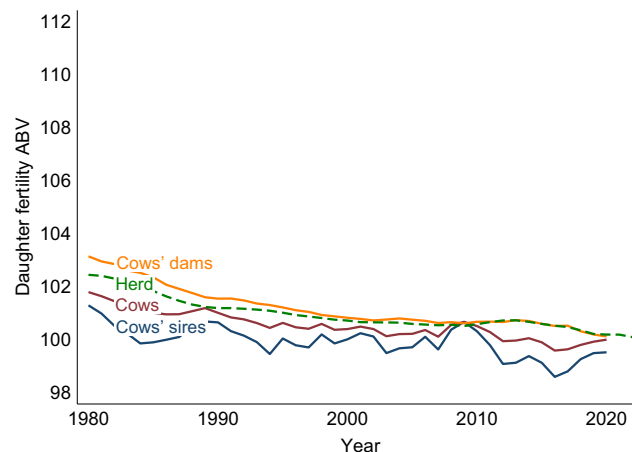
The corresponding graph for Jersey cows is shown in Fig. 3. There were small declines in mean daughter fertility ABVs for cows, cows' sires and cows' dams as cow's birth year increased from 1980 to 2020. Herd' means of cow daughter fertility ABVs declined from 102 for calvings in 1980 to 100 for calvings in 2022. Results for 2020-born cows for both breeds should be treated with caution as the numbers of cows in the dataset that were born in 2020 were considerably smaller than in previous years, and, of those, daughter fertility ABVs were available for low proportions (Table 1). The smaller numbers of 2020-born cows in the dataset may have been because additional 2020-born cows in study herds were still to calve and/or have their calving date entered into the central data repository when the study data were exported.
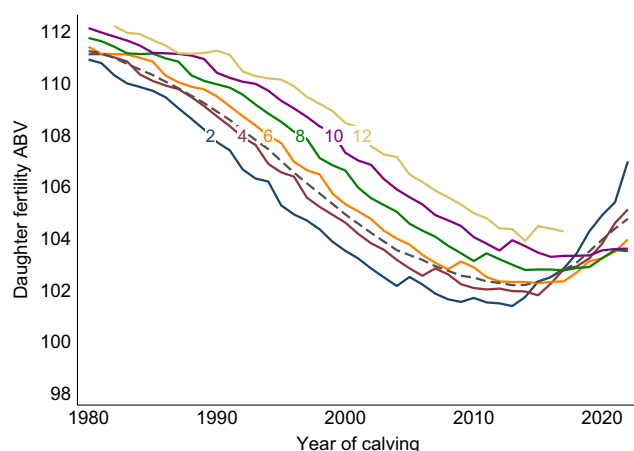
Given the marked changes in mean daughter fertility ABVs over time for Holsteins, trends were further explored for Holsteins. Cow means by year of calving were analysed by cow age at calving (Fig. 4). Means for 2-year-old cows calved in each year decreased until 2013, before increasing rapidly for 2-year-old cows that calved in subsequent years. For older age categories, nadirs for means were progressively later. Collectively, these patterns indicated that mean cow daughter fertility ABVs increased for cows born from 2011 and 2012. Herd means (dashed line) are the age-weighted averages of cows that calved in the year by cow age. These increased less rapidly than for 2-year-old calvings in each year due to delays until means for older cows ceased declining and increased.

Progressive effects of cow culling decisions on mean cow daughter fertility ABVs were also assessed (Fig. 5). For cohorts born in 1980 and 1985, mean cow daughter fertility ABVs for older cows still in the herd were similar to those for cows in the herd as 2-year olds, so there was no evidence of

Table 1. Numbers of calvings by cow birth year and cow age for calvings by Holstein cows by cow's age at calving (2–12 years) for eight birth cohorts (cow birth year from 1980 to 2015).
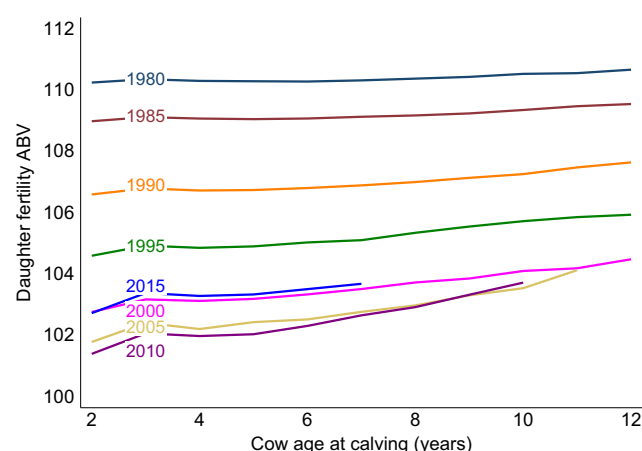
Cow birth year	Cow age at calving (years)					
	2	4	6	8	10	12
1980	15 880 (100%)	12 927 (81%)	9651 (61%)	6441 (41%)	3480 (22%)	1286 (8%)
1985	32 501 (100%)	24 922 (77%)	18 441 (57%)	12 242 (38%)	6086 (19%)	1880 (6%)
1990	41 445 (100%)	31 527 (76%)	22 811 (55%)	12 526 (30%)	5146 (12%)	1274 (3%)
1995	44 533 (100%)	33 061 (74%)	23 643 (53%)	12 137 (27%)	4759 (11%)	1075 (2%)
2000	48 180 (100%)	32 722 (68%)	22 575 (47%)	10 981 (23%)	3879 (8%)	1125 (2%)
2005	39 199 (100%)	25 905 (66%)	17 394 (44%)	8714 (22%)	3124 (8%)	600 (2%)
2010	26 231 (100%)	16 677 (64%)	10 676 (41%)	4802 (18%)	1467 (6%)	
2015	34 325 (100%)	20 826 (61%)	13 331 (39%)			

Percentages describe numbers of calvings by cows of the age shown as proportions of the number of calvings by 2-year-old cows in that birth cohort. Within birth cohorts, cow age categories with fewer than 1000 calvings were not included.

Fig. 4. Mean cow daughter fertility ABVs for calvings by Holstein cows by cow age at calving (2–12 years) in the year of calving shown. Means for all cows that calved by year ('herd means') are shown as the dashed line. Within cow age categories, years with fewer than 1000 calvings were not plotted.

Fig. 5. Mean cow daughter fertility ABVs for calvings by Holstein cows by cow's age at calving (2–12 years) for eight birth cohorts (cows born in each of 1980, 1985, 1990, 1995, 2000, 2005, 2010 and 2015). Numbers of cows enrolled in each birth cohort at their 2-year-old calving are shown in Table 1. Within each birth cohort, for each age at calving, only cows that calved at that age were included in the mean for that age. Within birth cohorts, cow age categories with fewer than 1000 calvings were not plotted.

selective retention of cows with higher daughter fertility ABVs. However, within subsequent birth cohorts, mean cow daughter fertility ABVs for older cows still in the herd were higher than for cows in the herd as 2-year olds, with greater differences within birth cohorts where the mean cow daughter fertility ABVs of 2-year olds was lower. Thus, cows with higher daughter fertility ABVs had been selectively retained, with a greater selection pressure in birth cohorts where the mean cow daughter fertility ABVs of 2-year olds was lower.

Percentages of cows that calved as 2-year olds that were still in the herd and calved at 4, 6, 8, 10 and 12 years of age are shown in Table 1. Percentages of 2-year olds that were retained to each of these age categories were markedly smaller in more recent cow birth-year cohorts,

cohorts where the mean cow daughter fertility ABVs of 2-year olds was lower.

Distributions of cow's sire daughter fertility ABVs

Distributions of cows' sire daughter fertility ABVs for Holstein cows by cow's year of birth are shown in Fig. 6. Median values were similar to means for sire ABVs as reported in Fig. 1 and for cows' sire ABVs as reported in Fig. 2. Variation in sire daughter fertility ABVs among cows progressively decreased for birth cohorts from 2010, but there was still considerable variation for more recently born cows. For example, for a
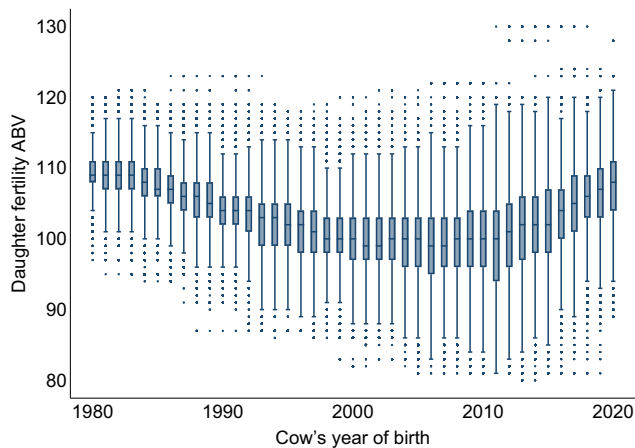
Fig. 6. Distribution of cows' sire daughter fertility ABV for Holstein cows by cow's year of birth. Boxes indicate the 25th and 75th percentiles, whiskers extend from these percentiles to the most extreme observed values that were ≤1.5 times the interquartile range below the 25th percentile and above the 75th percentile, and each value outside of the whiskers is shown as a dot. Bars in boxes are medians.

Fig. 7. Distribution of herd mean cow daughter fertility ABVs for calvings by Holstein cows by year of calving. Herd mean ABVs were used only for herd-years with at least 100 calvings by Holstein cows and where between 6% and 29% of those cows were aged <30 months, and between 29% and 54% of those cows were aged ≥60 months at that calving. Boxes indicate the 25th and 75th percentiles, whiskers extend from these percentiles to the most extreme observed values that were ≤1.5 times the interquartile range below the 25th percentile and above the 75th percentile, and each herd mean outside of the whiskers is shown as a dot. Bars in boxes are medians.

considerable proportion of cows born in 2020, the sire's daughter fertility ABVs were <100.

Distributions of herd mean daughter fertility ABVs

Distributions of herd mean cow daughter fertility ABVs for calvings by Holstein cows by year of calving are shown in Fig. 7. There was considerable variation in means among herds within each year of calving. For example, for 2021, herd means ranged from 98 to 111. Herd means were less variable for calvings earlier in the study period.

Assessment for selection bias due to herds entering and herds ceasing milk recording or dairying

Genetic trends shown in Figs 1–4, 6 are means for all sires or cows with data available for the year as shown. As herds enter and cease milk recording or dairying, means for successive years are not from the same population of herds. To assess the impact of this on the observed genetic trends, mean daughter fertility ABVs for Holstein cows' sires as depicted in Fig. 2 ('Cows' sires') were overlaid with means by cow birth years for sequential (i.e. rolling) 4- and 10-year cohorts (Figs S2, S3). Each 4- and 10-year cohort consisted only of cows from herds with data in all 4 or 10 years respectively. Means for these cohorts closely reflected means for all cows with data available for the year, indicating that the observed genetic trends using all available cows in each year were not substantially affected by systematic differences among herds that contributed to each mean in each year.
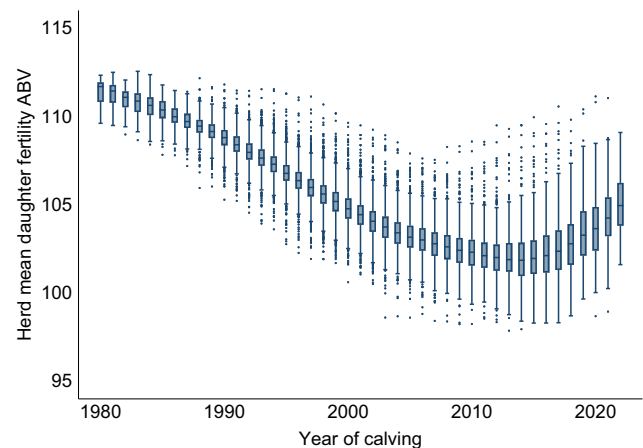
Discussion

Genetic trends in sires relative to trends in cows and herds

These results confirmed previous reports of marked deterioration in Holstein sires' daughter fertility estimated breeding values (VanRaden *et al.* 2004; Guinan *et al.* 2023). In the current study, declines were evident for sires born from 1980, the earliest year assessed. VanRaden *et al.* (2004) assessed genetic trends for daughter fertility in sires born from 1960 to 1999. For Holstein sires, deterioration was evident for that entire study period. daughter fertility ABVs declined much more slowly in Jerseys. Within Holsteins, rates of decline in daughter fertility ABVs were most rapid in sires, less rapid in cows and least rapid at herd level. This is as expected in self-replacing dairy herds due to the delay until older cows are culled and replaced with 2-year-old cows that are genetically inferior for the trait. Similarly, with genetic recovery, increases in daughter fertility ABVs were most rapid in sires, less rapid and somewhat delayed in cows, and least rapid and most delayed at herd level. Thus, genetic trends in sires were not closely related to genetic trends in herds. Further discordance was evident within sires where, from 1990 to 2010, means for cows' sires did not reflect means for all sires lagged by 2–3 years, as would be expected if cows' sires were representative of all sires born 2–3 years earlier. This unrepresentativeness was probably largely due to number of daughters per sire

being associated with sire daughter fertility ABV. There was large variation in numbers of daughters per sire in the study population (Table S1).

Impacts of genetic deterioration

The effects of this genetic deterioration on herd reproductive performance and cow longevity in Holstein herds in the Australian dairy industry were probably substantial. In an Australian study using Holstein cows, odds of pregnancy by Week 6 of the breeding period (a key measure in seasonal and split calving herds, the predominant calving systems used in Australia over the study period) increased by an estimated 1.2 for each 2.5-unit increase in cow's daughter fertility ABV (Morton et al. 2017). If 40% of cows become pregnant by Week 6, this equates to an increase of 1.7 percentage points per 1-unit increase in cow's daughter fertility ABV. The estimated effect from a more recent Australian study using Holstein cows was similar, with an estimated increase of 1.5 percentage points per 1-unit increase in cow's daughter fertility ABV (J. Morton, unpubl. data) and both results are qualitatively concordant with the estimated hazard ratio for conception up to Day 42 of the mating period for Holstein cows of 1.054 from a recent Australian study (Ooi et al. 2022). Given that 'herd' means of cow daughter fertility ABVs declined from 111 for calvings in 1980 to 102 for calvings in 2013, proportions of cows that became pregnant by Week 6 probably typically deteriorated by 13–16 percentage points over that time, in addition to likely deterioration before 1980. Results from the current study also demonstrated that there were large decreases in cow longevity over that time, with the percentage of cows remaining in the herd until they were at least 6 years of age declining from 61% of cows born in 1980 (where the mean cow daughter fertility ABV was about 111) to only 39% of cows born in 2015 (where the mean cow daughter fertility ABV was about 103; Table 1). While other factors may have contributed to this deterioration, given the high marginal economic value of increased longevity and the very limited voluntary culling when herd reproductive performance is poor, it seems likely that the decline in cow daughter fertility ABVs was a major contributor.

Given the negative genetic correlations between milk yield traits and fertility, it is most likely that this decline in sire daughter fertility ABVs in Holsteins occurred due to strong selection for milk yield traits without strong concurrent selection for fertility. Presumably, this resulted in more rapid increases in ABVs for milk traits than would have occurred if there had been concurrent selection for fertility. However, it seems unlikely that this selection strategy was economically optimal for low to moderate feed input pasture-based herds. Weightings for fertility and other non-production traits in the major Australian selection index, the balanced performance index (BPI), have been progressively increased over the past decade, reflecting a desire by the industry to put more emphasis on these traits,

presumably due to farmers' assessments of the relative value of marginal changes in the various traits. There is a particular need to understand the effects of increases in milk production-trait ABVs on herd milk production and profitability in pasture-based herds with lower feed inputs. In these production systems, herd feed inputs do not necessarily increase as herd genetic merits increase. Thus, increases in herd fat and protein production with herd genetic merit without increased herd feed inputs (O'Sullivan et al. 2020) must be due to factors such as improved feed conversion (due, for example, to lower cow liveweight (O'Sullivan et al. 2019) and/or higher milk fat and protein concentrations relative to lactose concentration (O'Sullivan et al. 2020) and greater pasture grazing pressure by high genetic merit cows (O'Sullivan et al. 2020).

Rate of genetic recovery

It is clear from these results that the decline in cow daughter fertility ABVs in Holsteins is being reversed, but recovery in the study population has been slow. In both sires and cows, rates of decline slowed for those individuals born from 2000, and the daughter fertility ABV was first released in Australia (and included in the national breeding index) in 2004. However, mean daughter fertility ABVs for sires continued to decline in successive birth cohorts of sires up to 2009 and cows continued to decline in successive birth cohorts of cows up to 2012. This was reversed with a steep upward trends for sires born from 2010 and for cows born from 2013. This was broadly similar to results reported by Ma et al. (2019) where genetic deterioration in cow conception rates was evident in successive cohorts of cows born up to 2007, followed by increases for cows born from 2008 to 2016. Guinan et al. (2023) also reported increases in genetic merit for fertility for cows born from the early 2000s. However, the rate of increase in the study by Guinan et al. (2023) was slow, with only 2 units of the 12-unit decrease for sires from 1975 being recovered by 2017. In contrast, for Holstein sires in the current study, the rate of increase in daughter fertility ABVs for sires born from 2010 was considerably greater than the rate of decline from 1980 to 2000, and 6 units of the 8-unit decline for sires from 1980 to 2000 had been recovered by 2017 (the most recent year of birth with substantial numbers of sires; Fig. 1, Table S1).

Despite this, recovery in the study population has been slow because, in a reversal of patterns when daughter fertility ABV is declining, when these are increasing, rates of increase in daughter fertility ABVs are most rapid in sires, less rapid in cows and least rapid in herds. Similarly, in the study by Ma et al. (2019), genetic merit for cow conception rate increased more slowly in cows than sires. In the current study, herd mean daughter fertility ABVs increased from 102 for calvings in 2013 to only 105 for calvings in 2022. Under current trends, it will be a

considerable time before the adverse effects of the decline in daughter fertility ABVs are fully reversed in Australian dairy herds. An even-more rapid rate of increase in sire daughter fertility ABVs would hasten this recovery. The rate of increase is likely to be enhanced with the move to selection of sires on the basis of genomic values (Wiggans *et al.* 2017; Guinan *et al.* 2023).

The greatly lower rate of decline in daughter fertility ABVs in Jerseys was presumably due to less selection pressure for milk production traits and possibly less genetic variation for fertility in this breed. Nevertheless, there is evidence of decline in daughter fertility ABVs within Jerseys and it would seem prudent to implement steps to prevent further declines in that breed.

Variation in daughter fertility ABVs between cows and herds

Variation in sire's daughter fertility ABVs among cows progressively decreased for female birth cohorts from 2010, but there was still considerable variation for more recently born cows. For example, for a considerable proportion of cows born in 2020, the sire's daughter fertility ABV was <100. From Fig. 7, there was substantial variation in herd means among herds, probably largely because some herd managers were putting substantially more weight on daughter fertility ABVs when selecting sires than were other herd managers. In herds with high mean daughter fertility ABVs in 2022, to avoid using sires with lower daughter fertility ABVs than their average cow, those sires were required to have had daughter fertility ABVs >110–111. From Fig. 4, to avoid using sires with lower daughter fertility ABVs than that of the average 2-year-old that calved in 2022, those sires were required to have had daughter fertility ABVs >107, and >104 for older cows.

Selection pressure for higher daughter fertility ABVs due to cow culling decisions and dam selection

These results also demonstrated that selection pressure for higher daughter fertility ABVs was occurring within Australian herds. For recent birth cohorts, older cows had higher daughter fertility ABVs, indicating that cows with higher daughter fertility ABVs had greater longevity than did cows with lower daughter fertility ABVs (Fig. 5). This is likely to have been due to selection pressure due to culling of cows that did not become pregnant or had prolonged times until becoming pregnant. The observation that, up to approximately 1995, mean daughter fertility ABVs for cow's dams declined less rapidly than did means for cows (Fig. 2) may have been because, in many herds, replacement heifers were born of those cows that conceived earliest in the herd's breeding period, cows that, on average, would be expected to have higher daughter fertility ABVs. However,

it is evident from Figs 2 and 5 that the effects of these selection pressures were minimal relative to the rapid decline in daughter fertility ABVs for sires.

Genetic monitoring

It is possible that genetic trends for fertility differ by country due to differences in sire-selection decisions. However, more generally, these trends in Holsteins probably demonstrate the effects of genetic selection solely (or heavily weighted) for milk production on traits that are negatively genetically correlated with milk production traits, and that undesired genetic deterioration can take a long time to correct at herd level. An important ongoing task for animal breeding is to identify traits that may become important for farmers and community in future and, yet, may be declining genetically under current selection decisions. Theoretically, selection based on breeding indices that use numerous ABVs reduces the risk of large deteriorations in particular traits, but a program of ongoing monitoring of genetic trends for a wide range of traits would allow early detection and prompt implementation of ameliorative actions should such deteriorations commence. Such monitoring is becoming more important with the more rapid genetic change associated with selection of sires on the basis of genomic values (Wiggans *et al.* 2017; Guinan *et al.* 2023). Monitoring of sires by sire's year of birth should be complemented by monitoring of cows' sires by cow's year of birth as means of cows' sires may not accurately reflect means of sires lagged by 2–3 years, as demonstrated in the current study.

Conclusions

In conclusion, there was a marked decline in daughter fertility ABVs in Holsteins in the Australian dairy industry; this decline had commenced by 1980 and probably commenced earlier. Rates of decline were most rapid in sires, less rapid in cows and least rapid at herd level. Thus, genetic trends in sires were not closely related to genetic trends in herds. Selection pressure for higher daughter fertility ABVs due to cow culling decisions was probably occurring within Australian herds, but any such effect was minimal relative to the rapid decline in daughter fertility ABVs for sires. This decline probably resulted in substantial reductions in herd reproductive performance and cow longevity in Holstein herds in the Australian dairy industry. The decline in cow daughter fertility ABVs is being reversed, but recovery of herd means in the study population has been slow, despite rapid increases in daughter fertility ABVs of sires used in recent years, and, under current trends, it will be a considerable time before the adverse effects of the decline in daughter fertility ABVs are fully reversed in Australian dairy herds. The rate of decline in daughter fertility ABVs in Jerseys was less than for Holsteins, but it would seem prudent to implement steps to prevent further declines in

that breed. An important ongoing task for animal breeding is to identify and monitor traits that may become important for farmers and community in future but may be declining genetically under current selection decisions.

Supplementary material

Supplementary material is available online.

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