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## INTERPRETIVE SUMMARY

2 **Effects of polled on yield and fitness traits.** *Cole and Null, page 0000.* This study  
3 examined the relationship of the polled (hornless) haplotype to phenotypic and genetic  
4 merit for traits of economic importance in U.S. Brown Swiss, Holstein, and Jersey cattle.  
5 Effects were generally small and none were statistically different from 0. Selection for  
6 polled cattle in these three breeds should not have a detrimental effect on yield, fertility,  
7 or longevity.

8 ***Short communication: Phenotypic and Genetic Effects of the***  
9 **Polled Haplotype on Yield, Longevity, and Fertility in U.S.**

10 **Brown Swiss, Holstein, and Jersey Cattle**

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**ABSTRACT**

21 Phenotypes from the December 2018 US national genetic evaluations were used  
22 to compute phenotypic effects of the polled haplotype in U.S. Brown Swiss (**BS**),  
23 Holstein (**HO**), and Jersey (**JE**) cattle on milk, fat, and protein yields, somatic cell score  
24 (**SCS**), single-trait productive life (**PL**), daughter pregnancy rate (**DPR**), heifer  
25 conception rate (**HCR**), and cow conception rate (**CCR**). Lactation records pre-adjusted  
26 for non-genetic factors and direct genomic values (**DGV**) were used to estimate  
27 phenotypic and genetic effects of the polled haplotype, respectively. No phenotypic or  
28 DGV effects were different from 0 for any trait in any breed. Genomic PTA (**gPTA**) for  
29 the lifetime net merit (**NM\$**) selection index of bulls born since January 1, 2012, that  
30 received a marketing code from the Nation Association of Animal Breeders, and cows  
31 born on or after January 1, 2015, were compared to determine if there was a systematic  
32 benefit to polled or horned genetics. Horned bulls had the highest average gPTA for NM\$  
33 in all three breeds, but that difference was significant ( $P < 0.05$ ) only in HO and JE (HO:  
34  $615.4 \pm 1.9$ , JE:  $402.3 \pm 3.4$ ). Homozygous polled BS cows had significantly higher  
35 average gPTA for NM\$ ( $P < 0.05$ ) than their heterozygous polled or horned  
36 contemporaries (PP =  $261.4 \pm 43.5$ , Pp =  $166.1 \pm 13.7$ , pp =  $174.1 \pm 1.8$ ), but the sample  
37 size was very low ( $n = 9$ ). In HO and JE, horned cows had higher gPTA for NM\$ ( $P <$   
38  $0.05$ ; HO =  $378.3 \pm 0.2$ , JE =  $283.3 \pm 0.3$ ). Selection for polled cattle should not have a  
39 detrimental effect on yield, fertility, or longevity, but these differences show that, in the  
40 short term, selection for polled over horned cattle will result in lower rates of genetic  
41 gain.

42 (**Keywords:** genomic evaluation, phenotypic effects, polled)

43           The rapid growth in the number of genotyped dairy cattle, which recently  
44 surpassed 3 million in the United States, has resulted in the identification of several  
45 recessive disorders, permitted the determination of carrier status of genotyped animals  
46 using haplotypes in place of laboratory tests (Cole et al., 2018), and enabled the  
47 calculation of haplotype effects on production and fitness traits (Cole et al., 2016).  
48 Schafberg and Swalve (2015) provide a comprehensive history of polled cattle, and there  
49 is increasing interest in the polled phenotype (e.g., Thompson et al., 2017) for purposes  
50 of improving animal welfare. Soller et al. (1963) reported an association between  
51 polledness and infertility in male Saanen goats, and there are anecdotal reports that polled  
52 dairy cattle also have reduced fertility compared to their horned counterparts. Several  
53 studies have shown that polled and horned cattle have similar genetic merit for calving,  
54 health, growth, and reproduction traits (Frisch et al., 1980; Goonewardene et al., 1999a,b;  
55 Kommisrud and Steine, 1997; Lamminger et al., 2000). However, polled Holstein cattle  
56 were shown to have lower average genetic merit than their horned contemporaries  
57 (Spurlock et al., 2014; Windig et al., 2015). The purpose of this study was to determine  
58 the phenotypic and genetic effects of the polled haplotype in the U.S. Brown Swiss,  
59 Holstein, and Jersey breeds on 8 yield and fitness traits.

60           The data used in this analysis consisted of phenotypes and direct genomic values  
61 (**DGV**) from the December 2018 US national genetic evaluation for genotyped daughters  
62 of genotyped bulls in the U.S. Brown Swiss, Holstein, and Jersey breeds. This ensured  
63 that polled haplotype status was known for both cows and bulls. The 8 traits included in  
64 this study were milk, fat, and protein yields, somatic cell score (**SCS**), single-trait  
65 productive life (**PL**), daughter pregnancy rate (**DPR**), heifer conception rate (**HCR**), and

66 cow conception rate (**CCR**). Cows were required to have phenotypes for all traits in the  
67 analysis, and the dataset included all lactations in the database except for PL and HCR,  
68 which have single (lifetime) values. Genotypes for all cows were imputed to a common  
69 set of 79,294 SNP used for US genomic evaluations with findhap.f90 version 3  
70 (VanRaden et al., 2011). Counts of bulls and cows by breed and polled haplotype status  
71 are provided in Table 1.

72       There are two distinct mutations on chromosome 1 responsible for polledness in  
73 taurine dairy cattle. An 80 kb deletion is responsible for most polled Holstein and Jersey  
74 cattle (Rothhammer et al., 2014), while a 212 bp indel is responsible for most polled beef  
75 and dual-purpose cattle (Medugorac et al., 2012). Polled status is sent by the genotyping  
76 laboratories but their reports do not distinguish between the two mutations, and older  
77 genotyping arrays included only SNP tracking the Friesian mutation. Most chips now  
78 include the Celtic haplotype, too, but a single tag SNP at 2,578,598 bp on chromosome 1  
79 is used to track both mutations in the US population. It is possible, in principle, to  
80 determine the specific polled mutation carried by an animal but, in practice, it is much  
81 easier to track and distribute to the industry general status (polled/horned) rather than the  
82 individual mutation carried. Most animals included in this study had direct genotypes (BS  
83 = 3,918; HO = 787,995; JE = 142,239) rather than imputed genotypes (BS = 127; HO =  
84 3,391; JE = 465).

85       A fixed-effects model was fitted to phenotypic and genetic values for all traits  
86 using PROC GLM in SAS 9.4 (TS1M2) for Linux (SAS Institute Inc., Cary, NC):

$$87 \quad y_{ijk} = \mu + \text{sire}_j + \text{status}_k + e_{ijk}$$

88 where  $y_{ijk}$  is the phenotypic value or DGV for each of the 8 traits evaluated for cow  $i$ ,  $\mu$  is  
89 the overall mean,  $sire_j$  is the fixed effect of the cow's sire,  $status_k$  is the fixed effect of the  
90 polled haplotype (coded as 0, 1, or 2 copies of the minor – polled – allele), and  $e_{ijk}$  is the  
91 random residual error term. Sire effects were absorbed, and the polled haplotype effect  
92 was tested for differences using a  $t$  test. Phenotypes were pre-adjusted for non-genetic  
93 factors by subtracting management group, parity-sex, and herd-by-sire effects from each  
94 observation. The DGV were calculated as the sum of individual SNP effects from the  
95 December 2018 genomic evaluation (Wiggans et al., 2011) plus breed- and trait-specific  
96 intercepts (Cole and Null, 2013). A within-trait Bonferroni adjustment was used to  
97 correct for multiple comparisons, and significance was declared when  $P < 0.0028$ .

98        Genomic PTA (**gPTA**) for the lifetime net merit selection index (**NM\$**;  
99 VanRaden et al., 2018) of bulls born since January 1, 2012, that received a marketing  
100 code from the Nation Association of Animal Breeders, and cows born on or after January  
101 1, 2015, were also compared to determine if there was a systematic benefit to polled or  
102 horned genetics. Bulls were restricted to those marketed because many young males are  
103 genotyped but never have semen available for sale, so they do not contribute to genetic  
104 trend in the next generation. Cows were selected to represent a cohort of contemporary  
105 animals that have had the opportunity to complete their first lactations.

106        The effects of the polled haplotype on the phenotypic and genetic values of the 8  
107 traits from are shown in Tables 2 and 3, respectively. P-values were adjusted on a within-  
108 trait basis to account for multiple comparisons. Of the 24 phenotype tests conducted,  
109 none were significant at the 0.0028 level (Bonferroni-adjusted within trait) or higher.  
110 None of the 24 DGV effects were different from 0. A significant haplotype effect would

111 not necessarily indicate a causal relationship, and an association of a genotype with trait  
112 differences could be due to hitchhiking. For example, Peñagaricano and Khatib (2012)  
113 found evidence that alleles with deleterious fertility effects are associated with milk  
114 protein genes, and concluded that the observed effects may be due to hitchhiking. These  
115 results are consistent with the findings of Gehrke et al. (2016), who reported that polled  
116 Holstein cattle in Germany had lower milk, fat, and protein yields than their horned  
117 contemporaries. Dressel et al. (2016) also found that polled German Holsteins had lower  
118 breeding values for milk yield and the total merit index.

119         Horned bulls had the highest average gPTA for NM\$ in all three breeds, but that  
120 difference was significant ( $P < 0.05$ ) only in HO and JE (HO:  $615.4 \pm 1.9$ , JE:  $402.3 \pm$   
121  $3.4$ ). Homozygous polled BS cows had significantly higher average gPTA for NM\$ ( $P <$   
122  $0.05$ ) than their heterozygous polled or horned contemporaries (PP =  $261.4 \pm 43.5$ , Pp =  
123  $166.1 \pm 13.7$ , pp =  $174.1 \pm 1.8$ ), but the sample size was very low ( $n = 9$ ). In HO and JE,  
124 horned cows had higher gPTA for NM\$ ( $P < 0.05$ ; HO =  $378.3 \pm 0.2$ , JE =  $283.3 \pm 0.3$ ).  
125 These differences suggest that, in the short term, selection for polled over horned cattle  
126 will result in lower rates of genetic gain. However, this could change rapidly if  
127 consumers and milk processors demand that management practices change to eliminate  
128 the need for disbudding. In such a case, the polled haplotype could have enough value to  
129 offset losses in lifetime profit attributable to increased production.

130         These results show that there is no association of the polled haplotype with yield,  
131 longevity, or fertility in U.S. BS, HO, or JE cattle. Selection for polled cattle in these  
132 breeds is unlikely to have a detrimental effect on performance unless polled families trace  
133 back to a narrow genetic base and genetic load accumulates in those lines. However, the

134 small pool of available polled animals limits the selection pressure which can be applied  
135 to that sub-population and will result in lower rates of genetic gain (e.g., Windig et al.,  
136 2015) until more polled bulls are available. Advanced reproductive or gene editing  
137 technologies (e.g., Mueller et al., 2019) can be used to increase the frequency of polled  
138 animals in these breeds without undesirable effects on the traits studied.

139

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## EFFECTS OF POLLED ON YIELD AND FITNESS TRAITS

217 **Table 1.** Number of unique bulls and cows included in each dataset by breed and polled haplotype status.

Dataset	Breed	Bulls			Cows		
		Polled (PP)	Polled (Pp)	Horned (pp)	Polled (PP)	Polled (Pp)	Horned (pp)
Phenotypes	BS	1	7	368	1	64	7,552
	HO	57	306	10,671	1,334	14,551	1,119,639
	JE	8	120	2,305	317	8,986	245,909
Direct genomic values	BS	30	893	28,828	5	50	3,990
	HO	1,394	8,908	256,418	908	10,316	780,162
	JE	117	1,515	29,244	312	5,302	137,090

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## EFFECTS OF POLLED ON YIELD AND FITNESS TRAITS

219 **Table 2.** Effect of the polled haplotype on phenotypes pre-adjusted for non-genetic factors of milk, fat, and protein yield,  
 220 somatic cell score (SCS), single-trait productive life (PL), daughter pregnancy rate (DPR), heifer conception rate (HCR), and  
 221 cow conception rate (CCR).

Breed <sup>1</sup>	Statistic	Trait							
		Milk (kg)	Fat (kg)	Protein (kg)	SCS	PL (mo)	DPR (%)	CCR (%)	HCR (%)
BS	N	7,617	7,617	7,617	7,358	2,229	4,428	4,428	4,428
	Effect	-277.11	-0.86	-4.75	0.31	-2.26	-4.73	11.22	-2.52
	SE	902.33	35.28	24.98	0.56	4.66	6.70	21.57	1.90
HO	N	1,135,524	1,135,524	1,135,524	1,109,327	396,166	615,215	615,215	615,215
	Effect	25.11	-2.99	-1.28	0.06	-0.55	0.82	4.87	-0.01
	SE	29.44	1.05	0.74	0.02	0.44	0.75	1.85	0.24
JE	N	255,212	255,212	255,212	252,672	81,301	196,942	196,942	196,942
	Effect	13.78	1.40	1.74	0.003	0.62	-0.85	-6.25	0.74
	SE	27.82	1.76	1.24	0.031	0.90	1.42	3.87	0.65

222 <sup>1</sup>BS = Brown Swiss, HO = Holstein, and JE = Jersey.

## EFFECTS OF POLLED ON YIELD AND FITNESS TRAITS

223 **Table 3.** Effect of the polled haplotype on direct genomic values of milk, fat, and protein yield, somatic cell score (SCS),  
 224 single-trait productive life (PL), daughter pregnancy rate (DPR), heifer conception rate (HCR), and cow conception rate  
 225 (CCR).

Breed <sup>1</sup>	Statistic	Trait							
		Milk (kg)	Fat (kg)	Protein (kg)	SCS	PL (mo)	DPR (%)	CCR (%)	HCR (%)
BS	N	4,045	4,045	4,045	4,045	4,045	4,045	4,045	4,045
	Effect	110.55	4.45	3.44	-0.06	0.05	-0.47	-0.18	0.12
	SE	45.44	1.72	1.26	0.03	0.42	0.33	0.33	0.30
HO	N	791,386	791,386	791,386	791,386	791,386	791,386	791,386	791,386
	Effect	3.82	-0.03	0.10	-0.004	0.05	0.05	0.06	0.07
	SE	3.84	0.14	0.09	0.002	0.03	0.03	0.03	0.02
JE	N	142,704	142,704	142,704	142,704	142,704	142,704	142,704	142,704
	Effect	4.04	-0.35	0.02	-0.001	-0.05	202.08	0.06	-0.08
	SE	5.13	0.20	0.14	0.003	0.04	0.04	0.04	0.03

226 <sup>1</sup>BS = Brown Swiss, HO = Holstein, and JE = Jersey.

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EFFECTS OF POLLED ON YIELD AND FITNESS TRAITS

228 **Table 4.** Least squares means of genomic predicted transmitting ability for lifetime net merit (\$) of homozygous polled (PP),  
 229 heterozygous polled (Pp), and horned (pp) bulls born on or after January 1, 2012, by breed<sup>1</sup>.

Breed <sup>1</sup>	Polled (PP)			Polled (Pp)			Horned (pp)		
	N	Mean <sup>2</sup>	SE	N	Mean	SD	N	Mean	SE
BS	3	211.7	73.3	12	262.3	36.6	275	273.5	7.6
HO <sup>3</sup>	171	422.5	16.2	510	488.3	9.4	12,095	615.4	1.9
JE	11	311.3 <sup>A</sup>	43.6	113	374.4 <sup>A</sup>	13.6	1,825	402.3	3.4

230 <sup>1</sup>BS = Brown Swiss, HO = Holstein, and JE = Jersey.

231 <sup>2</sup>Means sharing the same superscript did not differ from one another ( $P < 0.05$ ).

232 <sup>3</sup>All means within the row were different ( $P < 0.01$ ).

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EFFECTS OF POLLED ON YIELD AND FITNESS TRAITS

234 **Table 5.** Least squares means of genomic predicted transmitting ability for lifetime net merit (\$) of homozygous polled (PP),  
 235 heterozygous polled (Pp), and horned (pp) cows born on or after January 1, 2015, by breed.

Breed <sup>1</sup>	Polled (PP)			Polled (Pp)			Horned (pp)		
	N	Mean <sup>2</sup>	SE	N	Mean	SE	N	Mean	SE
BS	9	261.4	43.5	90	166.1 <sup>A</sup>	13.7	5,386	174.1 <sup>A</sup>	1.8
HO <sup>3</sup>	1,622	318.9	4.9	22,278	345.9	1.3	1,584,663	378.3	0.2
JE <sup>3</sup>	665	257.5	5.2	8,799	272.7	1.4	198,489	283.3	0.3

236 <sup>1</sup>BS = Brown Swiss, HO = Holstein, and JE = Jersey.

237 <sup>2</sup>Means sharing the same superscript did not differ from one another ( $P < 0.05$ ).

238 <sup>3</sup>All means within the row were different ( $P < 0.01$ ).