GENETICS AND BREEDING

Heterosis for Growth and Yield Traits from Crosses of Friesian Strains[1]

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ABSTRACT

Heterosis for growth and yield traits was estimated for F_1 and backcross generations that resulted from crosses of Holstein or Friesian bulls from Canada, Denmark, Israel, The Netherlands, New Zealand, Sweden, the United Kingdom, the US, and West Germany with Polish Black and White cows. Growth traits included BW at 6 and 12 mo and mean daily gain from birth to 6 mo and 6 to 12 mo for bulls and BW at 6, 12, and 18 mo and mean daily gain from birth to 6 mo, 6 to 12 mo, and 12 to 18 mo for heifers. Yield traits were first lactation 305-d milk and fat yields and fat percentage. For bulls, heterotic and additive effects were not significant for 6- and 12-mo BW and mean daily gains. However, heterotic and additive effects for heifers were highly significant for 6- and 12-mo BW and mean daily gain from birth to 6 mo. Heterotic and additive effects were highly significant for milk and fat yields, but only additive effects were significant for fat percentage. Heterosis relative to the Polish mean was greatest for the Canadian strain (about 110% for milk and fat yields) and the US strain (106% for milk yield and 110% for fat yield).

(**Key words**: heterosis, Friesian, crossbreeding, growth)

Abbreviation key: FAO = Food and Agriculture Organization, **UK** = United Kingdom.

INTRODUCTION

Genetic superiority of North American Holstein cattle for milk yield over Friesian strains has been demonstrated in many studies (1, 3, 9, 10, 14). For growth and beef production, the situation is more complex. Although Holsteins grow faster and have greater mature size, the quality of their carcasses usually is scored lower (3, 7).

Genetic differences among strains for yield and growth traits have been evaluated in several trials. One of the largest trials on Friesian strain comparison was conducted in Poland under the auspices of the Food and Agriculture Organization (**FAO**) of the United Nations (3, 12, 13). Other studies with fewer strains and animals (1, 2, 10) yielded similar results. As a consequence of these studies, a great increase in Holstein semen importation and use in the majority of European Friesian cattle populations has occurred in recent years.

Less information is available from those trials on heterosis for yield traits and BW. In reviews of crossbreeding experiments, Pearson and McDowell (8), Turton (14), and McDowell (5) concluded that, although estimates of heterosis vary considerably, positive heterosis exists for BW up to second calving and for milk and fat yields. Heterotic effects seldom existed for milk composition (component percentages).

Objectives of this study were to estimate heterotic effects for BW and dairy performance based on F_1 crosses and backcrosses to foreign bulls produced as part of the FAO trial in Poland.

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MATERIALS AND METHODS

The design and experimental procedures of the FAO trial on comparison of Friesian strains have been described in detail (3, 12, 13). Nine cooperating countries [Canada, Denmark, Israel, New Zealand, Sweden, The Netherlands, the United Kingdom (UK), the US, and West Germany] sent frozen semen from 348 young unproven AI bulls to Poland in 1974 (168 bulls) and in 1975 (180 bulls). In addition to these bulls, semen from 40 Polish bulls was used. Inseminations of Polish Black and White cows to produce the F_1 generation started in March 1974 and were completed by the end of 1976. To obtain backcross generations with 75% foreign genes and 25% Polish genes, only semen sent in 1975 was used to inseminate F_1 cows between May 1976 and March 1978. A backcross group with 75% Polish genes also was produced but is not included in this study because of its small size. The experiment was designed to compare additive genetic values of strains and provided only limited data for a direct comparison of F_1 and backcross animals.

Growth traits included BW and daily gains calculated from data recorded during the FAO trial (3, 12, 13); birth weight was not included as a trait because some weightings occurred up to 2 d after birth. For bulls, BW at 6 and 12 mo were included, and mean daily gains were calculated from birth to 6 mo and from 6 to 12 mo. Bulls were not castrated and were not selected. For heifers, BW at 6, 12, and 18 mo of age were included, and mean daily gains were calculated for each age interval. All BW were standardized for age at weighing (6, 12, or 18 mo) by regression within strain. Yield traits were first lactation 305-d milk and fat yields and fat percentage; fat yield was determined by applying fat percentage to milk yield.

A linear mixed model was used for yield traits and mean daily gains:

$$y_{ijklm} = \mu + c_{ij} + s_{ik} + g_l + b_l(t_{ijklm} - \bar{t}) + e_{ijklm}$$

where y_{ijklm} is an observation in herd-year-season l for progeny m resulting from cross j to sire k of strain i, μ is overall mean, c_{ij} is fixed effect of strain i and cross j (j = 1 for F_1, 2 for backcross, or 3 for 100% Polish), s_{ik} is random effect of sire k within strain i (with mean 0 and variance-covariance matrix $\mathbf{I}\sigma_s^2$, where $\mathbf{I}$ is an identity matrix), g_l is fixed effect of weighting or calving for herd-year-season l, t_{ijklm} is age in days at weighing or calving for progeny m, $\bar{t}$ is mean age at weighing or calving, b_l is a coefficient of regression of trait on age at weighing or calving, and e_{ijklm} is random residual (normally distributed with mean 0 and variance-covariance matrix $\mathbf{I}\sigma_e^2$). For analyses of standardized BW, regression on age at weighing was removed from the linear model. Ratios of error variance to sire variance added to the sire submatrix diagonal were based on mean heritabilities estimated for the Polish Black and White population (15) and were assumed to be .25 for all traits.

A relationship matrix was not included in the model because the objective was to estimate fixed strain effects. These strain effects correspond to group effects in sire evaluation. Inclusion of a complete relationship matrix when all parents and pedigrees are known makes grouping unnecessary. If relationship information is incomplete (as in this study), group effects become difficult to analyze and to interpret (11). In the original FAO strain comparison (3, 13), the largest relationships between strains were estimated to be 2.3% between Canadian and West German bulls and 1.6% between US and Israeli bulls; relationships among bulls were less than .8% between all other strains.

Estimates of strain additive genetic (a_i) and heterotic (h_i) effects were calculated from the mathematical expectation of strain effects as follows:

$$E\begin{bmatrix}\hat{c}_{i1}\\ \hat{c}_{i2}\end{bmatrix} = \begin{bmatrix}.5a_i + h_i\\ .75a_i + .5h_i\end{bmatrix} = \begin{bmatrix}.5 & 1\\ .75 & .5\end{bmatrix}\begin{bmatrix}a_i\\ h_i\end{bmatrix};$$

$$\begin{bmatrix}\hat{a}_i\\ \hat{h}_i\end{bmatrix} = \begin{bmatrix}.5 & 1\\ .75 & .5\end{bmatrix}^{-1}\begin{bmatrix}\hat{c}_{i1}\\ \hat{c}_{i2}\end{bmatrix} = \begin{bmatrix}-1 & 2\\ 1.5 & -1\end{bmatrix}\begin{bmatrix}\hat{c}_{i1}\\ \hat{c}_{i2}\end{bmatrix},$$

where E is the mathematical expectation, $\hat{c}_{i1}$ and $\hat{c}_{i2}$ are estimates of fixed effect for strain i and F_1 cross (c_{i1}) and strain i and backcross (c_{i2}), $\hat{a}_i$ is estimate of additive genetic effect of strain i relative to the Polish strain, and $\hat{h}_i$ is estimate of h_i relative to the Polish strain. Backcrosses from strains with higher annual genetic gain would be expected to have higher genetic merit because of the use of semen sent only in 1975. However, quantification of differences in genetic trend between 1974 and 1975 would be difficult, and, therefore, genetic trend was not considered in estimation of additive and heterotic effects.

Percentage of heterosis relative to the Polish strain (h%) was calculated as

$$h\% = [(\bar{y}_{parent} + \hat{h}_i)/\bar{y}_{parent}] (100),$$

where $\bar{y}_{parent}$ (parent mean) = $[\bar{y}_{Poland} + (\bar{y}_{Poland} + \hat{a}_i)]/2 = \bar{y}_{Poland} + .5\hat{a}_i$, $\bar{y}_{Poland}$ is raw trait mean for the Polish strain, and $\bar{y}_{Poland} + \hat{a}_i$ is trait mean for strain i. Therefore, a relative heterosis of 100% would indicate no heterosis.

Significance of a_i and h_i was determined by examining **Bc** where **c** is the vector of strain × cross effects (c_{ij}) and **B** for a_i is the 9 × 19 matrix

$$\begin{bmatrix} -1 & 2 & & & & & & & 0 \\ & & -1 & 2 & & & & & 0 \\ & & & & \ddots & \ddots & & & \vdots \\ & & & & & & -1 & 2 & 0 \end{bmatrix},$$

and **B** for h_i is the 9 × 19 matrix

$$\begin{bmatrix} 1.5 & -1 & & & & & & & 0 \\ & & 1.5 & -1 & & & & & 0 \\ & & & & \ddots & \ddots & & & \vdots \\ & & & & & & 1.5 & -1 & 0 \end{bmatrix}.$$

An approximate *F* test was constructed with an assumed known variance ratio in the mixed model:

$$F = [(\mathbf{B}\hat{\mathbf{c}})'(\mathbf{B}'\mathbf{D}_{11}\mathbf{B})^{-1}(\mathbf{B}\hat{\mathbf{c}})/r(\mathbf{B})]/\hat{\sigma}_e^2,$$

where $\hat{\mathbf{c}}$ is estimated **c**; $\mathbf{D}_{11}$ is the part of the inverse for the mixed model equations that corresponds to **c**; r(**B**), the rank of **B**, is 9; and $\hat{\sigma}_e^2$ is the estimated error variance component.

RESULTS AND DISCUSSION

Comparison of F_1 and Backcross Generations

Numbers of backcross animals were much smaller than for the F_1 generation (Tables 1, 2, and 3). Animal numbers differ from those reported for the FAO trial by Jasiorowski et al. (3) because only animals with a complete set of BW were included for growth traits and because records from the state dairy recording system (rather than farm records) were used for yield traits. Numbers of bulls were greater than numbers of heifers because of involuntary culling and exclusion of animals with missing BW. Animal losses were similar in F_1 and backcross generations for all strains (3).

Means for growth traits for bulls generally were higher for the F_1 generation than for the backcross generation, regardless of strain, whereas standard deviations often were slightly larger. For the Israeli strain, mean BW at 6 mo and mean daily gain from birth to 6 mo were higher for the backcross than for the F_1 generation. Means for BW for heifers (Table 2) also generally were higher for the F_1 than for the backcross generation except for heifers of the UK strain at 6, 12, and 18 mo; heifers of The Netherlands strain at 12 and 18 mo; and heifers of the Israeli and West German strains at 18 mo. Mean daily gains of F_1 heifers were lower than for backcross heifers for The Netherlands, UK, and US strains from birth to 6 mo; for the Israeli, The Netherlands, UK, and US strains from 6 to 12 mo; and for all strains except UK and US from birth to 18 mo. In general, differences in daily gains between F_1 and backcross generations were relatively small; the largest difference was 36 g for the Canadian strain between 12 and 18 mo.

For all strains, mean milk and fat yields decreased for the backcross generation (Table 3); standard deviations generally increased for milk yield and decreased for fat yield. For milk yield, coefficients of variation ranged from 26 to 28% for F_1 crosses and were 3 to 6% higher for backcrosses, usually 29% or more (except for The Netherlands crosses, which had the same coefficients of variation for both generations). The pattern was similar for fat yield. Largest differences between F_1 and backcross generations for milk yield were 559 kg for the US strain, 529 kg for the West German strain,

TABLE 1. Mean BW and daily gains and standard deviations for F_1 and backcross bulls by age of bull and strain.

Strain	Generation	Number	BW				Daily gain in BW			
			6 mo		12 mo		Birth to 6 mo		6 to 12 mo	
			(kg)				(g)			
			$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Canada	F_1	768	171	20	299	36	725	110	701	157
	Backcross	88	162	23	288	38	691	120	690	161
Denmark	F_1	742	168	21	295	37	711	113	698	162
	Backcross	83	165	23	290	38	709	124	688	161
Israel	F_1	731	172	20	300	36	734	110	705	159
	Backcross	92	173	24	298	40	750	126	690	184
New Zealand	F_1	709	168	20	297	36	714	106	711	159
	Backcross	85	160	23	281	36	681	121	665	170
Sweden	F_1	727	169	20	298	36	718	110	709	154
	Backcross	87	166	19	286	35	716	97	660	155
The Netherlands	F_1	703	166	20	290	36	707	111	679	156
	Backcross	77	159	23	281	38	681	121	669	190
United Kingdom	F_1	701	168	21	295	36	716	112	697	158
	Backcross	88	158	21	280	36	679	112	668	180
US	F_1	697	170	20	300	36	718	104	715	160
	Backcross	75	163	23	287	35	695	126	680	173
West Germany	F_1	778	168	20	296	37	712	111	704	161
	Backcross	88	162	20	290	40	700	106	704	185
Poland (purebred)	. . .	1536	168	21	296	37	720	114	705	162

and 526 kg for The Netherlands strain; largest differences for fat yield were 26 kg for the US strain, 23.8 kg for the New Zealand strain, and 23.4 kg for the Israeli strain. Smallest differences were 278 kg for milk and 15.2 kg for fat for the Danish strain and 285 kg for milk and 15.9 kg for fat for the Swedish strain.

Lower BW for both bulls and heifers and lower milk and fat yields for the backcross generation resulted from adverse environmental conditions from 1981 through 1982. Reduced availability of feed depressed performance, as was evidenced by backcross performance of contemporary pure Polish cows (3).

Additive and Heterotic Effects

Growth Traits. Additive and heterotic effects for growth traits are in Tables 4 and 5 for bulls. No additive or heterotic effects for BW (Table 4) and mean daily gain (Table 5) were significant ($P > .05$) overall. Oldenbroek (6) also found no heterotic effects for BW for crosses of The Netherlands Friesians with Holsteins. For BW of bulls at 6 mo (Table 4), heterosis expressed as a percentage of Polish strain mean (100%) was about 104% for the Canadian strain, 102% for the US strain, and slightly over 100% for the New Zealand and West German strains; for other strains, heterosis was slightly below 100%. Relative heterosis for 12-mo BW of bulls varied even less. Estimates were between 102% for the Canadian and US strains and 99.4% for the Israeli strain. Relative heterosis for mean daily gains in BW of bulls from birth to 6 mo (Table 5) also was slightly higher for the Canadian (102.8%) and US (100.1%) strains than for other strains (96.8 to 99.3%). Relative heterosis for mean daily gain from 6 to 12 mo was over 100% for all strains except Canadian, The Netherlands, and US; the Swedish strain had the highest relative heterosis at 103%. Although heterosis estimates for the Israeli strain generally were below 100%, additive effects were large. Results from the original Polish trial (3, 13) indicated a high ranking for the Israeli strain: the US, Canadian, and Israeli strains had the largest positive effects for 12-mo BW and mean daily gain from birth to 12 mo for F_1 males, whereas positive effects were largest for the Israeli and West German strains for backcross males.

TABLE 2. Mean BW and daily gains and standard deviations of F_1 and backcross heifers by age of heifer and strain.

Strain	Generation	Number	BW						Daily gain in BW					
			6 mo		12 mo		18 mo		Birth to 6 mo		6 to 12 mo		12 to 18 mo	
			(kg)						(g)					
			$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Canada	F_1	551	160	16	275	22	370	25	673	88	634	106	517	124
	Backcross	88	152	17	264	22	365	27	648	93	614	106	553	144
Denmark	F_1	587	156	18	271	23	368	26	661	99	630	107	533	122
	Backcross	76	150	16	260	23	360	27	642	87	604	119	543	128
Israel	F_1	585	160	17	274	22	370	26	679	93	632	114	524	128
	Backcross	70	154	16	271	23	371	30	666	91	640	116	544	155
New Zealand	F_1	673	158	16	273	22	368	24	670	87	634	110	518	122
	Backcross	117	152	17	266	20	365	25	650	98	627	98	540	140
Sweden	F_1	599	158	17	272	22	368	26	674	94	621	115	526	125
	Backcross	97	154	18	267	22	367	25	662	97	616	122	551	124
The Netherlands	F_1	571	156	17	269	24	365	26	665	90	622	109	522	124
	Backcross	65	155	17	271	20	367	26	670	94	638	109	524	117
United Kingdom	F_1	604	156	16	269	23	366	26	659	86	625	104	527	125
	Backcross	62	156	18	272	22	366	26	673	96	640	120	510	124
US	F_1	488	158	16	271	23	370	24	663	89	626	107	537	128
	Backcross	64	155	17	270	21	367	27	670	98	630	112	530	134
West Germany	F_1	601	159	16	275	22	368	25	675	87	638	108	509	122
	Backcross	99	155	16	271	19	369	25	666	92	636	100	536	124
Poland (purebred)	. . .	1175	156	17	272	22	366	26	668	93	632	106	518	123

TABLE 3. Mean milk and fat yields and fat percentage and standard deviations for F_1 and backcross cows by strain.

Strain	Generation	Number	Milk yield		Fat yield		Fat percentage	
			(kg)				(%)	
			$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Canada	F_1	616	3695	970	147.5	39.9	3.98	.30
	Backcross	131	3373	1030	128.9	38.4	3.85	.32
Denmark	F_1	633	3370	900	136.0	38.2	4.02	.29
	Backcross	114	3092	1030	120.8	44.1	3.88	.34
Israel	F_1	641	3713	980	148.2	39.7	3.97	.32
	Backcross	109	3257	980	124.8	39.6	3.80	.31
New Zealand	F_1	698	3576	940	147.1	39.4	4.11	.34
	Backcross	155	3103	932	123.3	39.3	3.97	.35
Sweden	F_1	674	3442	890	138.3	38.2	3.99	.28
	Backcross	137	3157	930	122.4	36.9	3.88	.33
The Netherlands	F_1	608	3264	860	131.8	36.2	4.03	.29
	Backcross	96	2738	710	109.5	30.5	3.99	.35
United Kingdom	F_1	638	3380	940	135.5	38.5	4.01	.29
	Backcross	101	2992	1030	119.0	40.9	3.92	.33
US	F_1	568	3788	1060	149.9	43.2	3.93	.29
	Backcross	85	3229	1020	123.9	41.4	3.82	.31
West Germany	F_1	653	3332	920	133.8	36.6	3.99	.29
	Backcross	132	2803	960	113.9	38.8	3.90	.35
Poland (purebred)	. . .	1308	3184	880	128.5	36.9	4.01	.28

TABLE 4. Additive and heterotic effects for BW of bulls by age of bull and strain.

Strain	BW at 6 mo						BW at 12 mo					
	Heterosis[1]	SE	Additive effects[2]	SE	Heterotic effects	SE	Heterosis[1]	SE	Additive effects[2]	SE	Heterotic effects	SE
	(%)		(kg)				(%)		(kg)			
Canada	103.9	1.2	-4.2	3.7	6.5	2.1	101.6	1.2	-.4	6.2	4.6	3.4
Denmark	99.1	1.2	3.3	3.8	-1.5	2.1	99.8	1.2	-1.1	6.3	-.6	3.5
Israel	98.9	1.2	12.6	3.6	-1.9	2.0	99.4	1.1	14.7	6.0	-1.9	3.4
New Zealand	100.5	1.3	-3.3	3.8	.8	2.1	100.6	1.2	-2.1	6.3	1.9	3.5
Sweden	99.8	1.2	4.4	3.7	-.4	2.1	101.1	1.2	.1	6.2	3.3	3.4
The Netherlands	99.8	1.3	.4	4.0	-.4	2.2	99.7	1.2	-3.9	6.6	-.8	3.6
United Kingdom	99.9	1.2	.9	3.7	-.2	2.1	100.2	1.2	-1.8	6.2	.5	3.4
US	101.8	1.3	.2	4.0	3.0	2.2	101.5	1.2	1.1	6.7	4.6	3.7
West Germany	100.2	1.2	2.7	3.7	.3	2.1	99.5	1.1	8.7	6.2	-1.6	3.4

[1]100% indicates no heterosis.

[2]Relative to Polish (purebred) mean.

Additive and heterotic effects for growth traits for heifers are in Tables 6 and 7. Additive and heterotic effects for 6- and 12-mo BW were highly significant ($P < .01$) overall (Table 6). Relative heterosis was highest for BW of Canadian (105.6% at 6 mo; 103.2% at 12 mo) and New Zealand (104.4% at 6 mo; 101.0% at 12 mo) heifers. Relative heterosis was lower than the Polish mean for the UK strain for all BW (97.0 to 99.9%) and for The Netherlands strain for 12- and 18-mo BW (97.9 and 99.8%). Additive effects also were highly significant ($P < .01$) overall for 6- and 12-mo BW; maximum effects were negative for the Canadian strain (-9.3 kg at 6 mo; -8.6 at 12 mo) and positive for the US (5.1 kg at 6 mo) and UK strains (14.6 kg at 12 mo). For 18-mo BW, heterotic and additive effects were not significant ($P > .05$) overall, and estimates of relative heterosis ranged from 99.8 to 103.2%. For two-breed cattle crosses, several researchers [see reviews by McAllister (4), Pearson and McDowell (8), and Turton (14)] reported heterotic effects for BW and growth in the range of 3 to 6.5%; as in the present study, heterotic effects usually decreased with age.

Ranking of strains based on additive effects for heifer BW varied at different ages. The US strain was first at 6 and 18 mo but fifth at 12

TABLE 5. Additive and heterotic effects for mean daily gains in BW of bulls by age of bull and strain.

Strain	Mean daily gain from birth to 6 mo						Mean daily gain from 6 to 12 mo					
	Heterosis[1]	SE	Additive effects[2]	SE	Heterotic effects	SE	Heterosis[1]	SE	Additive effects[2]	SE	Heterotic effects	SE
	(%)		(g)				(%)		(g)			
Canada	102.8	1.6	-11.4	20.0	19.9	11.1	98.6	2.2	15.1	28.5	-10.1	15.7
Denmark	96.8	1.5	32.6	20.6	-23.6	11.4	100.7	2.3	-24.4	29.3	5.0	16.2
Israel	97.6	1.4	75.6	19.6	-18.6	10.9	100.0	2.2	11.3	27.9	-.3	15.5
New Zealand	99.3	1.6	-4.9	20.4	-4.8	11.3	100.8	2.2	7.0	27.4	5.8	15.4
Sweden	98.6	1.5	31.9	20.1	-10.1	11.2	102.9	2.3	-23.6	28.5	20.1	15.9
The Netherlands	98.7	1.6	17.6	21.4	-9.8	11.8	99.7	2.4	-23.6	30.4	-2.2	16.7
United Kingdom	98.7	1.5	18.4	20.0	-9.2	11.2	100.5	2.3	-14.7	28.5	3.7	15.9
US	100.1	1.6	12.8	21.7	.4	11.9	101.2	2.4	5.2	30.8	8.4	16.9
West Germany	97.6	1.5	39.9	20.0	-17.6	11.0	98.6	2.2	32.9	28.4	-10.5	15.7

[1]100% indicates no heterosis.

[2]Relative to Polish (purebred) mean.

TABLE 6. Additive and heterotic effects for BW of heifers by age of heifer and strain.

Strain	BW at 6 mo						BW at 12 mo						BW at 18 mo					
	Heterosis[1]	SE	Additive effects[2,3]	SE	Heterotic effects[3]	SE	Heterosis[1]	SE	Additive effects[2,3]	SE	Heterotic effects[3]	SE	Heterosis[1]	SE	Additive effects[2]	SE	Heterotic effects	SE
	(%)		(kg)				(%)		(kg)				(%)		(kg)			
Canada	105.6	1.2	-9.3	3.1	8.5	1.8	103.2	.9	-8.6	4.3	8.5	2.5	103.2	.8	-10.9	4.7	11.4	2.7
Denmark	102.1	1.2	-5.1	3.3	3.3	1.9	101.6	1.0	-5.6	4.6	4.3	2.6	102.2	.8	-9.9	5.1	8.0	2.8
Israel	102.4	1.2	.2	3.5	3.7	1.9	100.7	1.0	5.7	4.8	2.0	2.7	101.5	.8	.5	5.3	5.5	2.9
New Zealand	104.1	1.0	-8.5	2.7	6.2	1.6	101.0	.8	.7	3.8	2.6	2.2	100.9	.7	-1.8	4.2	3.2	2.4
Sweden	102.9	1.1	-2.1	3.0	4.5	1.7	100.1	.9	2.0	4.1	.4	2.4	100.7	.7	1.0	4.5	2.4	2.6
The Netherlands	100.2	1.3	-2.1	3.6	.3	2.0	97.9	1.0	8.0	5.0	-5.7	2.8	99.8	.8	1.6	5.5	-.9	3.0
United Kingdom	98.9	1.3	3.6	3.7	-1.8	2.0	97.0	1.0	14.6	5.1	-8.4	2.8	99.9	.8	1.8	5.6	-.3	3.1
US	100.0	1.3	5.1	3.6	0	2.0	100.5	1.0	3.5	5.1	1.3	2.8	101.5	.8	3.4	5.5	5.4	3.1
West Germany	102.4	1.1	-1.0	2.9	3.8	1.7	100.6	.9	6.2	4.1	1.5	2.3	101.3	.7	1.1	4.5	4.8	2.6

[1]100% indicates no heterosis.

[2]Relative to Polish (purebred) mean.

[3]Effect significant overall ($P < .01$).

TABLE 7. Additive and heterotic effects for mean daily gains in BW of heifers by age of heifer and strain.

Strain	Mean daily gain from birth to 6 mo						Mean daily gain from 6 to 12 mo						Mean daily gain from 12 to 18 mo					
	Heterosis[1]	SE	Additive effects[2,3]	SE	Heterotic effects[3]	SE	Heterosis[1]	SE	Additive effects[2]	SE	Heterotic effects	SE	Heterosis[1]	SE	Additive effects[2]	SE	Heterotic effects	SE
	(%)		(g)				(%)		(g)				(%)		(g)			
Canada	105.5	1.5	-46.6	16.8	35.6	9.6	100.0	1.9	4.0	20.9	0	12.0	103.2	2.5	-12.8	22.4	16.1	12.8
Denmark	101.4	1.5	-21.7	18.0	9.0	10.0	100.9	2.0	-2.4	22.4	5.8	12.5	104.0	2.7	-23.7	24.0	20.2	13.4
Israel	102.7	1.6	-1.5	18.7	17.8	10.4	98.6	2.0	30.0	23.3	-9.2	13.0	103.9	2.8	-28.6	25.0	19.4	13.9
New Zealand	104.4	1.3	-41.7	14.6	28.3	8.4	97.0	1.6	50.3	18.2	-19.8	10.5	100.6	2.2	-13.7	19.4	3.2	11.2
Sweden	103.4	1.4	-13.9	16.0	22.4	9.1	96.5	1.8	22.5	19.9	-22.8	11.4	102.2	2.4	-5.2	21.3	11.2	12.2
The Netherlands	100.0	1.6	-7.9	19.4	-.1	10.7	95.0	2.0	55.8	24.2	-33.0	13.4	105.2	2.9	-34.7	25.9	26.0	14.3
United Kingdom	97.8	1.6	28.1	19.8	-15.3	10.9	94.5	2.1	60.3	24.7	-36.3	13.6	109.1	3.0	-69.8	26.5	43.9	14.5
US	98.6	1.6	28.7	19.6	-9.6	11.0	101.1	2.2	-8.5	24.4	6.9	13.7	104.3	2.8	-.8	26.2	22.4	14.6
West Germany	101.9	1.4	-1.3	15.8	12.5	9.1	98.1	1.7	39.9	19.7	-12.1	11.3	103.5	2.4	-28.3	21.1	17.7	12.1

[1]100% indicates no heterosis.

[2]Relative to Polish (purebred) mean.

[3]Effect significant overall ($P < .01$).

mo. The Canadian strain ranked last for all three ages, and all additive effects were negative. The Israeli strain ranked third at 6 mo, fourth at 12 mo, and sixth at 18 mo. The US, UK, and Israeli strains had higher additive effects for all ages, whereas the Canadian strain was lowest. Using separate analyses for F_1 and backcross generations, Stolzman et al. (13) found positive strain effects for birth, 12-mo, and 18-mo heifer BW for US, Canadian, West German, and Israeli strains and generally negative effects for the UK strain.

Estimates of heterotic effects showed consistent superiority for heifer BW for the Canadian strain; estimates were lowest for the UK and The Netherlands strains. Differences between US and Canadian strains in the magnitude and direction of additive effects resulted in the largest estimates of relative heterosis for BW in the Canadian strain. This consistent difference between US and Canadian Holstein strains is difficult to explain.

Mean daily gain in heifer BW between birth and 6 mo (Table 7) showed significant ($P < .01$) overall heterotic and additive effects. Estimates of relative heterosis were similar to those for 6-mo BW. Largest relative heterosis was 105.5% for the Canadian strain; lowest was 97.8% for the UK strain. Heterotic and additive effects for mean daily gains between 6 and 12 mo and between 12 and 18 mo were not significant ($P > .05$) overall.

Yield Traits. For yield traits (Table 8), additive and heterotic effects were highly significant ($P < .01$) overall for milk and fat yields; additive effects also were significant ($P < .01$) overall for fat percentage. Heterotic effects for milk and fat yields were similar to or slightly higher than those reported by several researchers (5, 8, 9, 14).

For milk yield, the Canadian strains had the highest relative heterosis (110.7%) and heterotic effects (350 kg), followed by The Netherlands (106.5%, 200 kg) and US (106.3%, 211 kg) strains. Largest additive effect was 755 kg for the Israeli strain, which also had the largest negative heterotic effect (–95 kg); relative heterosis for the Israeli strain was 97.3%. Next largest additive effects were 409 kg for the New Zealand strain, 376 kg for the Swedish strain, 280 kg for the US strain, and 203 kg for the Canadian strain. Jasiorowski et al. (3) reported the largest positive effects for the US, Canadian, and Israeli strains for both F_1 and backcross generations and estimated heterosis for the US and Canadian strains as 8% of the mean milk yield of Polish cows.

For fat yield, ranking of strains was slightly different. The Canadian strain again had the highest relative heterosis (110.4%) and heterotic effects (13.6 kg) but was followed by the US (109.6%, 12.9 kg) and New Zealand (104.2%, 5.8 kg) strains. The UK strain has the largest negative heterotic effect (–6.2 kg). Again, the additive effects were largest (25.9 kg) for the Israeli crosses followed by the UK (21.6 kg), New Zealand (20.7 kg), Swedish (16.6 kg), and US (11.7 kg) strains. In the Jasiorowski et al. (3) study, positive effects were largest for the US, Canadian, New Zealand, and Israeli strains for the F_1 and backcross generations; heterosis was estimated as 9% of mean fat yield for Polish cows for the US and Canadian strains.

Relative heterosis for fat percentage was slightly lower than for milk and fat yields but above the Polish mean for all strains; heterosis ranged from 100.4% for the Swedish strain to 105.6% for The Netherlands strain. Additive effects for fat percentage were small and negative for all strains compared with the Polish strain, which had low yield and consequently higher fat percentage; Israeli, West German, Danish, and US strains had the lowest additive effects. Heterotic effects for fat percentage were small, positive, and nonsignificant ($P > .05$) overall. Jasiorowski et al. (3) reported the largest positive effect for the New Zealand strain for the F_1 generation; strain effect on fat percentage for the backcross generation was nonsignificant ($P > .05$).

CONCLUSIONS

Relative heterosis for growth traits for crosses of Holstein or Friesian strains with Polish Black and White cattle was low for bulls and only slightly higher for heifers. For milk and fat yields, crosses with North American Holsteins showed sizable relative heterosis (6.3 to 10.7% above parent mean). Estimates for heterotic effects were based on more animals than in many of the previous studies (2, 5, 8, 10, 14). The magnitude of these estimates could indicate existence of heterosis for milk and fat yields.

TABLE 8. Additive and heterotic effects for yield traits of cows by strain.

Strain	Milk yield						Fat yield						Fat percentage					
	Heterosis[1]	SE	Additive effects[2,3]	SE	Heterotic effects[3]	SE	Heterosis[1]	SE	Additive effects[2,3]	SE	Heterotic effects[3]	SE	Heterosis[1]	SE	Additive effects[2,4]	SE	Heterotic effects	SE
	(%)		(kg)				(%)		(kg)				(%)					
Canada	110.7	8.1	203	323	350	246	110.4	6.1	5.5	10.5	13.6	7.3	101.2	1.8	-.143	.100	.046	.070
Denmark	100.9	8.0	29	340	30	255	99.5	5.5	8.3	10.5	-.7	7.4	102.4	1.8	-.192	.100	.092	.068
Israel	97.3	6.4	755	302	-95	229	101.8	4.3	25.9	9.5	2.6	6.0	101.7	1.6	-.213	.092	.068	.060
New Zealand	100.6	6.6	409	287	21	221	104.2	4.7	20.7	9.2	5.8	6.2	102.7	1.6	-.068	.088	.106	.060
Sweden	98.1	6.5	376	291	-65	222	98.4	5.0	16.6	9.6	-2.2	6.8	100.4	1.7	-.097	.092	.015	.066
The Netherlands	106.5	9.4	-243	363	200	274	100.0	5.7	2.4	11.1	0	7.4	105.6	1.8	-.001	.108	.025	.072
United Kingdom	98.8	7.8	130	346	-39	255	95.5	5.3	21.6	11.1	-6.2	7.6	100.9	1.7	-.058	.102	.025	.067
US	106.3	7.9	280	340	211	252	109.6	6.0	11.7	10.6	12.9	7.4	100.7	1.8	-.190	.102	.027	.071
West Germany	100.7	6.9	109	289	24	222	99.4	5.3	8.5	10.1	-.8	7.1	101.9	1.8	-.198	.096	.073	.068

[1]100% indicates no heterosis.

[2]Relative to Polish (purebred) mean.

[3]Effect significant overall ($P < .01$).

[4]Effect significant overall ($P < .05$).

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