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[1]*College of Agriculture and Veterinary Medicine, King Saud University, Saudi Arabia and*
[2]*Faculty of Agriculture at Moshtohor, Zagazig University, Egypt*
[3]*Animal Production Research Institute, Ministry of Agriculture, Egypt*

Estimation of heterotic components for lactation traits and reproductive performance in three crossbreeding trials of Holstein cattle with German Friesian raised under hot climatic conditions

By M. H. KHALIL[1], E. A. AFIFI[2], M. A. SALEM[2] and S. M. ZAHED[3]

Summary

Lactation traits and reproductive performance of three trials of crossing Holstein cattle (H) and German Friesians (F) raised in a hot climatic were evaluated. The first 90-day (M90), 305-day (M305) and total milk yield (TMY), 305-day milk yield per day of calving interval (MCI1), total milk yield per day of calving interval (MCI2) along with length of lactation period (LP), age at first calving (AC1) and calving interval (CI) were used. For these traits, a genetic model was applied for each trial separately to obtain estimates of individual (G^I) and maternal (G^M) additive effects, individual (H^I) and maternal (H^M) heterosis and individual recombination effect (R^I). Data of 8045 normal lactations from the three trials were analysed. Among the crossbreds obtained in the three trials, cows of $^3/_4H^1/_4F$ ranked first in their lactational performance. Estimates of G^I and G^M were generally large and in favour of H cows (daughters) and dams for most milk-yield traits, CI and AC1 in the three trials. Estimates of H^I in crossbred cows for milk traits, CI and AC1 were mostly negative and reveal that crossing F with H was associated with a reduction in milk-yield traits, shorter CI and earlier AC1 along with longer LP in the three trials. Estimates of H^M for milk yields, LP, AC1 and CI in daughters of crossbred dams were mostly negative. Recombination losses in crossbred cows were negative for milk-yield traits, AC1 and CI in most cases.

Zusammenfassung

Schätzung von Heterosiswirkungen in Merkmalen der Laktation und Fruchtbarkeit in 3 Kreuzungsversuchen zwischen Holstein Friesian und Dt. Schwarzbunten unter heißen klimatischen Bedingungen

Es wurden drei Versuche mit Kreuzungen zwischen Holstein (H) und deutschen Schwarzbunten (F) in heißem klima ausgewertet, wo 90 Tage (M90), 305 Tage (M305) und Gesamtmilchleistung (TMY), Tagesmilchleistung während des 303 Tage Intervalls (MCI1) und während der Zwischenkalbezeit, Länge der Laktationsperiode (LP), Erstkalbealter (AC1) und Zwischenkalbezeit (CI) untersucht worden sind. Es wurden geschätzt, für jeden Versuch separat, individuelle (G^I) und matennale (G^M) additive Wirkungen, individuelle (H^I) und maternale Heterosiswirkungen sowie individuelle Rekombinationswirkung (R^I). Daten von 8045 normalen Laktationen konnten analysiert werden. Rückkreuzungen zu H ($^3/_4H$ $^1/_4F$) zeigten unterKreuzungen die höchsten Leistungen. Additive Wirkungen, individuelle und maternale, ware groß und zugunsten H für die meisten Leistungseigenschaften, individuelle Heterosis für diese und CI sowie AC1 meistens negativ, sodaß Kreuzungen von H und F nicht empfohlen werden. Dies resultierte in weniger Milch, kürzeres CI und frühere AC1 mit längerem LP. Rekombinationsverlust war negativ für Milchleistung, AC1 und CI in den meisten Fällen.

Introduction

In the establishment of large-scale commercial dairy herds in Egypt, a common trend started in the early 1980s with the introduction of some standard breeds (e.g. Holstein, Friesian, Brown Swiss, Pinzgauer, etc.) to these herds. However, Holsteins and Friesians are superior in their individual and maternal additivity for milk yield traits (ROBISON et al. 1981; MARTINEZ et al. 1988; MADALENA et al. 1990a; AHLBORN-BREIER and HOHENBOKEN 1991; THORPE et al. 1993; ARAFA 1996). In temperate zones, many European and American

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studies (e.g. DONALD et al. 1977; ROBISON et al. 1981; RINCON et al. 1982; LIN et al. 1984; MARTINEZ et al. 1988; PEDERSEN and CHRISTENSEN 1989; MADALENA et al. 1990a, b; AHLBORN-BREIER and HOHENBOKEN 1991; TOUCHBERRY 1992; AKBAS et al. 1993; BOICHARD et al. 1993; THORPE et al. 1993; ZARNECKI et al. 1993; MCALLISTER et al. 1994) showed that crossbred cows which included Holstein and/or Friesian blood relative to other crossbreds exhibited a greater superiority in milk production and reproductive performance. In addition, the genetic superiority of Holsteins over different Friesian strains for milk yield has been demonstrated by POLITIEK and KORTER (1982) and PEDERSEN and CHRISTENSEN (1989). In hot or tropical climate zones, genetic analysis of milk-yield traits and/or reproductive performance in crossbreeding experiments between Holsteins (H) and Friesians (F) has not been attempted (MARTINEZ et al. 1988; MADALENA et al. 1990a; THORPE et al. 1993; ARAFA 1996; ARAFA et al. 1998).

The objective of the present study was to quantify breed group differences, additive effects (individual and maternal), heterotic effects (individual and maternal) and individual recombination loss for lactation and reproductive traits in three trials of crossbreeding Holstein cattle with German Friesians when raised under hot climatic conditions.

Material and methods

Animals and data

Friesian (F) and Holstein (H) cows and bulls have been imported from Germany to Egypt since 1980 by three commercial herds. The three herds are located in Fayoum Governorate (Upper Egypt), Gharbia Governorate (Lower Egypt) and Giza Governorate (Mid Egypt). All three herds belong to the General Cooperative for Developing Animal Wealth and Products (GCDAWP). All the imported females were pregnant heifers. Animals used in the present study comprised only locally born F and H purebred males and females as well as their crossbreds. Crossbreeding between F and H was started in the three herds at the beginning of 1981. Data of the three crossbreeding trials were collected over a period of 10 consecutive years (1985–1994). Each crossbreeding trial involved the production of F and H purebreds and their crosses of $^1/_2H^1/_2F$, $^3/_4F^1/_4H$, $^3/_4H^1/_4F$ and $^1/_4H^3/_4F$ (sire-breed listed first). Pedigrees of cows in terms of sires and dams in these commercial herds were not recorded. A total of 5460, 1756 and 829 normal lactation records were collected in Fayoum, Gharbia and Giza, respectively.

Management and feeding

In all herds, heifers and cows were largely naturally mated and sometimes artificially inseminated. The numbers of naturally serviced cows used in the various times were not available since service bulls were not recorded in the three farms. But in some few cases of reproductive disorders AI was practised. Heifers were bred when 16–18 months of age (about 350–375 kg) and cows were served during the first heat period following the 45th day post-partum. Pregnancy was detected by rectal palpation 60 days after the last service. Calves were given colostrum 4 days after birth, housed in calf-boxes and bucket-fed on milk and/or milk replacer until weaning at 90 kg weight for male calves and 100 kg for females. After weaning and up to 6 months of age, calves of the same age were group-housed in pens provided with yards for exercise. At 6 months of age, the male calves were separated from females and housed in open sheds up to sexual maturity.

In the three trials cows were machine-milked two or three times daily. Cows were usually milked until 2 months before the expected next date of calving. Then, if they did not go dry, they were dried off gradually by milking them once a day until completely dried off.

In the three herds, cows were kept under similar feeding and management sysems. All year round, all cows were fed concentrates and corn silage. During the winter and spring months (from December to May) the animals were supplied with Egyptian clover (*Trifolium alexandrinum*) and during summer and autumn months (from June to the end of November) beets, maize and green sorghum (*Sorghum vulgar*) were available. In addition, rice straw was available all the year round. Feed was supplied to cows according to their live weight, production and pregnancy status. Free clean water and mineral mixture were available at all times.

Traits investigated

Productive traits under study were 90-day milk yield considered as initial milk yield (M90), 305-day milk yield (M305), total milk yield (TMY), 305-day milk yield per day of calving interval (MCI1), total milk yield per day of calving interval (MCI2) and duration of lactation period (LP). Reproductive traits included age at first calving (AC1) and calving interval (CI). Milk yield was recorded to the nearest 0.1 kg daily at each milking. Age at calving was recorded in months, and duration of LP and CI were recorded in days. All abnormal records and those of aborted cows were excluded from the data. Ages of cows were classified into age subclasses of 3-month intervals, whereas duration of days open were grouped into subclasses of 20-day intervals.

Models of analysis

Data of each crossbreeding trial were analysed separately using the mixed model least squares and maximum likelihood program of Harvey (1990). Distribution of records for different genotypes in different years is represented in Figure 1. Data of the first lactation was analysed using the following linear model:

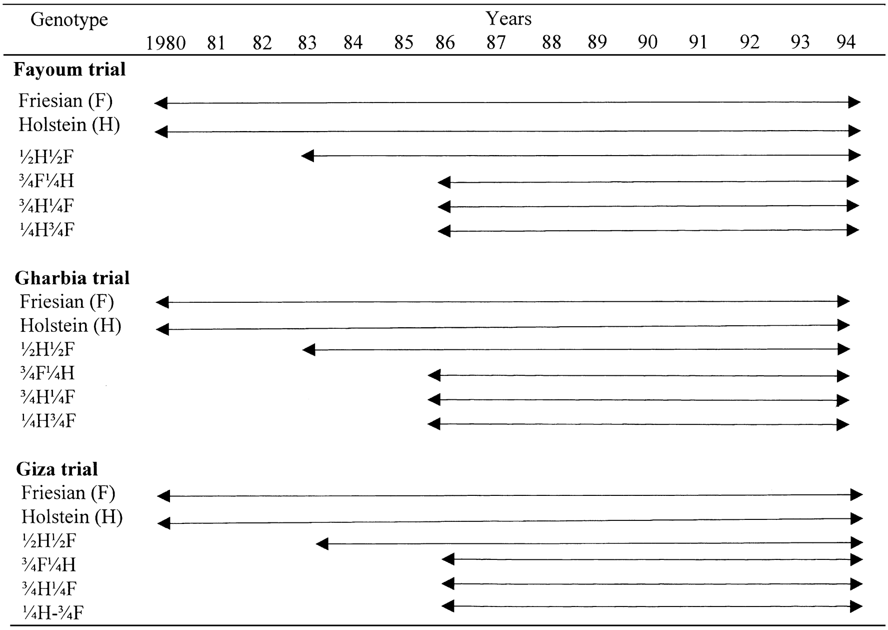

Fig. 1. Distribution of genotypes in different years

Table 1. **Model components used in the analysis of each crossbreeding trait separately**

Trait†	Model components
First lactation:	
M90, M305, TMY, LP, MCI1 and MCI2	Breed group (F), year–season–frequency of milking (F), age of cow at first calving (F), days open (F).
CI	Breed group (F), year–season–frequency of milking (F), age of cow at first calving (F).
AC1	Breed group (F), year–season of birth (F).
All lactations:	
M90, M305, TMY, LP, MCI1 and MCI2	Breed group (F), cows within breed group (R), year–season–frequency of milking (F), age of cow at calving (F), days open (F).
CI	Breed group (F), cows within breed group (R), year–season–frequency of milking (F), age of cow at calving (F).

† Traits as defined in Material and Methods
F, fixed effect; R, random effect

$$\mathbf{Y} = X\mathbf{B} + \mathbf{e}$$

and those of all lactations by:

$$\mathbf{Y} = X\mathbf{B} + Z\mathbf{U} + \mathbf{e}$$

where: **Y** is an $(n \times 1)$ observational vector, X is the incidence matrix for fixed effects, **B** is the vector of fixed effects (the fixed effects specified in Table 1 were considered for each trait). Z is the incidence matrix for random effects, **U** is the vector of random effects (cow effects), and **e** is the vector of random error.

Estimation of genetic components of crossbreeding effects

DICKERSON (1992) described the methodology of estimating the gneetic components from data of crossbreeding trials. According to DICKERSON's theory, the following genetic components were obtained: $\mathbf{G^I}$, the average individual (direct) additive effect of cow; $\mathbf{G^M}$, the average maternal additive effect of the dam of cow; $\mathbf{H^I}$, the expected individual heterosis in the crossbred cow, i.e. direct heterosis; $\mathbf{H^M}$, the expected heterosis in the crossbred dam, i.e. maternal heterosis; $\mathbf{R^I}$, the expected recombination effect in the individual cow, i.e. direct recombination loss.

The models presented above were used to derive a selected set of linear contrasts to estimate different heterotic components of G^I, G^M, H^I, H^M and R^I. The coefficients for these genetic components were computed as functions of the proportion of genes obtained from each strain or breed that contributed to the genotypes of the individuals (I) of each genetic group, their dams (M) and their sires (P). The coefficients for individual (G^I) and maternal (G^M) additive effects were calculated as the deviation of the proportion of **H** genes ($\mathbf{g^I_H}$) from the propotion of the F genes (g^I_F), i.e. $G^I = g^I_H - g^I_F$ and $G^M = g^M_H - g^M_F$, where g^I_H, g^I_F, g^M_H and g^M_F represent the proportion of H and F genes in the individual (I) and dam (M). The coefficients for individual (H^I) and maternal (H^M) heterosis were calculated for crossbred daughters and dams, respectively. The coefficients for individual recombination effect (R^I) were calculated for crossbred cows with blod proportion of $^3/_4$F or $^3/_4$H. Coefficients presenteed in Table 2 for the expected contribution of genetic effects (in F or H and their crosses) were computed according to DICKERSON (1992).

Table 2. **Coefficients of expected contribution for genetic effects in groups of purebreds and crossbreds**

Sire genotype	Dam genotype	Cow genotype†	Direct additive (g^{I}_{H-F})	Maternal additive (g^{M}_{H-F})	Direct heterosis (H^{I})	Maternal heterosis (H^{M})	Recombination effect (R^{I})
Friesian (F)	Friesian (F)	Friesian (F)	−1.0	−1.0	0.0	0.0	0.0
Holstein (H)	Holstein (H)	Holstein (H)	1.0	1.0	0.0	0.0	0.0
H	F	$^{1}/_{2}H^{1}/_{2}F$	0.0	−1.0	1.0	0.0	0.0
F	$^{1}/_{2}H^{1}/_{2}F$	$^{3}/_{4}F^{1}/_{4}H$	−0.50	0.0	0.50	1.0	0.25
H	$^{1}/_{2}H^{1}/_{2}F$	$^{3}/_{4}H^{1}/_{4}F$	0.50	0.0	0.50	1.0	0.25
$^{1}/_{2}H^{1}/_{2}F$	F	$^{1}/_{4}H^{3}/_{4}F$	−0.50	−1.0	0.50	0.0	0.25

† Sire-breed listed first

Results and discussion

Trends obtained from analysis of data of the first lactation were very similar to those obtained from data of all lactations. Therefore, results discussed here involved only results of all lactations.

Genetic-group comparison

Crossing Friesians (F) with Holsteins (H) in the three trials was always associated with the presence of significant differences between genetic groups for different lactation traits (Tables 3 and 4). DONALD et al. (1977), RINCON et al. (1982), MADALENA et al. (1990a), MCALLISTER et al. (1994), THORPE et al. (1994) and ARAFA (1996) also reported significant effects of genetic group on some milk traits.

Crossing F with H in the three trials show that M90, M305, TMY, MCI1 and MCI2 increased with the increase in the proportion of H blood from $^{1}/_{4}$H to $^{3}/_{4}$H (Tables 3 and 4), whereas an inconsistent trend was observed for LP. For most lactation traits in the three crossing trials, $^{3}/_{4}H^{1}/_{4}F$ always surpassed other crossbreds obtained, i.e. cows of $^{3}/_{4}H^{1}/_{4}F$ ranked first in their lactational performance. However, increasing the H blood in the genetic group led to a state in which H was superior in additive effects (MARTINEZ et al. 1988; BOICHARD et al. 1993). For different crosses between H and Zebu cattle in Brazil, MARTINEZ et al. (1988) indicated that performance of crossbreds in terms of M305 and MCI1 were improved as the percentage of H genes increased up to 50%. BOICHARD et al. (1993) found that for H crossed with European Black and White cattle the milk-yield traits in crossbreds increased with the increase of H blood.

For different crtossbreds across the three trials, no definite trend for AC1 and CI with the increase of proportion of H blood was observed (Tables 3 and 4). MARTINEZ et al. (1988) found that performance of crossbreds in terms of CI were improved as the percentage of H genes increased up to 50%.

Table 3. **Least-square means and their standard errors for milk and reproductive traits of the first lactation in different genetic groups**

		M90 (kg)	M305 (kg)	TMY (kg)	MCI1 (kg per day)	MCI2 (kg per day)	LP (day)	CI (day)	AC1 (month)
Breed group†	No.	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Fayoum trial									
Friesian (F)	98	1535 ± 31	3426 ± 104	3998 ± 126	8.35 ± 0.28	9.62 ± 0.31	345 ± 3	389 ± 7	27.7 ± 0.38
Holstein (H)	262	2366 ± 31	5734 ± 102	6737 ± 124	14.37 ± 0.27	16.56 ± 0.30	360 ± 3	414 ± 7	27.9 ± 0.31
$^{1}/_{2}$H$^{1}/_{2}$F	189	1753 ± 30	4164 ± 98	4860 ± 119	10.42 ± 0.26	11.91 ± 0.29	352 ± 3	408 ± 7	29.2 ± 0.33
$^{3}/_{4}$F$^{1}/_{4}$H	74	1559 ± 36	3471 ± 120	4043 ± 146	8.40 ± 0.32	9.76 ± 0.35	338 ± 4	372 ± 8	25.3 ± 0.40
$^{3}/_{4}$H$^{1}/_{4}$F	171	1831 ± 30	4429 ± 99	5012 ± 121	11.01 ± 0.26	12.33 ± 0.29	342 ± 3	407 ± 7	27.2 ± 0.32
$^{1}/_{4}$H$^{3}/_{4}$F	40	1704 ± 46	3964 ± 153	4615 ± 185	9.93 ± 0.41	11.30 ± 0.45	349 ± 5	401 ± 11	28.1 ± 0.58
Significance		***	***	***	***	***	***	***	***
Gharbia trial									
Friesian (F)	89	1746 ± 46	3862 ± 130	4280 ± 143	9.76 ± 0.36	10.54 ± 0.39	330 ± 5	379 ± 8	28.7 ± 0.44
Holstein (H)	57	2027 ± 57	4810 ± 158	5224 ± 175	12.25 ± 0.44	13.18 ± 0.47	318 ± 6	381 ± 10	27.4 ± 0.60
$^{1}/_{2}$H$^{1}/_{2}$F	41	1836 ± 57	4407 ± 158	4746 ± 175	10.97 ± 0.44	11.96 ± 0.48	318 ± 6	390 ± 10	27.1 ± 0.64
$^{3}/_{4}$F$^{1}/_{4}$H	60	1748 ± 63	3896 ± 176	4274 ± 194	9.64 ± 0.49	10.42 ± 0.53	323 ± 6	361 ± 11	29.7 ± 0.60
$^{3}/_{4}$H$^{1}/_{4}$F	29	1961 ± 69	4474 ± 192	5023 ± 213	11.30 ± 0.54	12.62 ± 0.58	327 ± 7	378 ± 12	27.7 ± 0.76
$^{1}/_{4}$H$^{3}/_{4}$F	54	1735 ± 45	4044 ± 126	4428 ± 140	10.25 ± 0.35	11.03 ± 0.38	318 ± 4	383 ± 8	27.8 ± 0.47
Significance		***	***	**	***	***	***	NS	NS
Giza trial									
Friesian (F)	35	1570 ± 63	3524 ± 212	4156 ± 239	8.65 ± 0.57	10.00 ± 0.63	343 ± 6	387 ± 13	28.7 ± 0.86
Holstein (H)	30	2258 ± 84	5427 ± 286	6127 ± 322	14.12 ± 0.77	15.50 ± 0.84	341 ± 8	359 ± 17	26.4 ± 1.15
$^{1}/_{2}$H$^{1}/_{2}$F	10	1897 ± 110	4511 ± 372	5094 ± 419	11.23 ± 1.01	12.62 ± 1.10	337 ± 11	361 ± 23	26.0 ± 1.35
$^{3}/_{4}$F$^{1}/_{4}$H	53	1647 ± 55	3864 ± 185	4566 ± 208	9.73 ± 0.50	11.37 ± 0.54	360 ± 5	405 ± 11	29.9 ± 0.83
$^{3}/_{4}$H$^{1}/_{4}$F	12	2030 ± 97	5116 ± 329	5999 ± 370	13.05 ± 0.89	14.99 ± 0.97	356 ± 10	387 ± 19	31.4 ± 1.45
$^{1}/_{4}$H$^{3}/_{4}$F	24	1701 ± 68	3924 ± 230	4530 ± 259	9.53 ± 0.63	10.74 ± 0.68	338 ± 7	417 ± 14	27.6 ± 0.96
Significance		***	***	***	***	***	NS	*	*

† Sire-breed listed first; NS, non significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

Table 4. **Least-square means and their standard errors for milk and reproductive traits of all lactations in different genetic groups**

		M90 (kg)	M305 (kg)	TMY (kg)	MCI1 (kg per day)	MCI2 (kg per day)	LP (day)	CI (day)
Breed group†	No.	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
Fayoum trial								
Friesian (F)	536	1695 ± 22	3976 ± 74	4612 ± 91	9.75 ± 0.18	11.21 ± 0.21	347 ± 1	412 ± 2
Holstein (H)	1371	2661 ± 21	6736 ± 71	7885 ± 87	16.37 ± 0.17	18.95 ± 0.20	350 ± 1	437 ± 2
$^1/_2$H$^1/_2$F	1227	1945 ± 17	4832 ± 58	5624 ± 72	11.95 ± 0.14	13.76 ± 0.17	353 ± 1	417 ± 2
$^3/_4$F$^1/_4$H	348	1710 ± 27	3997 ± 91	4583 ± 112	9.88 ± 0.22	11.27 ± 0.26	342 ± 1	416 ± 3
$^3/_4$H$^1/_4$F	830	2025 ± 24	5094 ± 81	5838 ± 99	12.56 ± 0.19	14.26 ± 0.23	345 ± 1	427 ± 3
$^1/_4$H$^3/_4$F	248	1861 ± 33	4537 ± 112	5260 ± 138	11.32 ± 0.17	12.97 ± 0.32	351 ± 2	428 ± 4
Significance		***	***	***	***	***	***	***
Gharbia trial								
Friesian (F)	590	1918 ± 38	4564 ± 111	5088 ± 118	11.33 ± 0.30	12.45 ± 0.31	331 ± 2	372 ± 3
Holstein (H)	232	2298 ± 52	5744 ± 153	6182 ± 163	14.42 ± 0.41	15.35 ± 0.43	321 ± 3	376 ± 4
$^1/_2$H$^1/_2$F	151	2118 ± 56	5188 ± 163	5627 ± 174	13.02 ± 0.44	13.94 ± 0.46	322 ± 3	377 ± 5
$^3/_4$F$^1/_4$H	392	2008 ± 47	4910 ± 140	5529 ± 149	12.20 ± 0.37	13.56 ± 0.40	338 ± 2	371 ± 3
$^3/_4$H$^1/_4$F	123	2219 ± 62	5307 ± 183	5807 ± 195	13.32 ± 0.49	14.40 ± 0.52	326 ± 3	373 ± 5
$^1/_4$H$^3/_4$F	268	2021 ± 46	4899 ± 135	5328 ± 143	12.22 ± 0.36	13.11 ± 0.38	322 ± 2	376 ± 3
Significance		***	***	***	***	***	***	NS
Giza trial								
Friesian (F)	183	1635 ± 57	3777 ± 191	4730 ± 201	9.31 ± 0.52	10.65 ± 0.54	345 ± 2	386 ± 4
Holstein (H)	86	2559 ± 72	6498 ± 240	7366 ± 254	16.65 ± 0.66	18.59 ± 0.69	351 ± 4	392 ± 7
$^1/_2$H$^1/_2$F	52	2098 ± 99	5276 ± 329	6100 ± 347	13.27 ± 0.90	15.17 ± 0.94	353 ± 4	387 ± 9
$^3/_4$F$^1/_4$H	295	1794 ± 53	4302 ± 175	4969 ± 186	10.72 ± 0.48	12.25 ± 0.50	349 ± 2	390 ± 4
$^3/_4$H$^1/_4$F	76	2101 ± 90	5476 ± 299	6224 ± 316	13.51 ± 0.82	15.37 ± 0.86	357 ± 4	408 ± 8
$^1/_4$H$^3/_4$F	137	1828 ± 67	4432 ± 222	4120 ± 235	10.98 ± 0.61	12.54 ± 0.63	348 ± 3	397 ± 5
Significance		***	***	***	***	**	*	NS

† Sire-breed listed first; NS, non-significant; *, $p < 0.05$; **. p 0.01; ***, $p < 0.001$

Table 5. **Estimates of individual additive effects (G^I) for different traits in the first and all lactations in the three crossing trials**

	Fayoum trial		Gharbia trial		Giza trial	
Trait[a]	Estimate	SE	Estimate	SE	Estimate	SE
First lactation:						
M90	1011***	50	442***	123	954***	126
M305	2904***	187	1339***	343	2765***	424
TMY	3355***	239	1435***	379	2963***	477
LP	16.4**	6.4	−7.4NS	12.0	−1.1NS	12.5
MCI1	7.6***	0.5	3.6***	1.0	7.9***	1.1
MC12	8.5***	0.6	4.0***	1.0	8.2***	1.2
CI	41.6**	31.1	8.4NS	22.1	−51.8*	26.2
AC1	−0.9NS	0.7	−2.2NS	1.3	−1.1NS	2.0
All lactations:						
M90	1185***	13	524***	38	1165***	30
M305	3472***	43	1481***	109	3515***	97
TMY	4087***	49	1365***	122	3909***	106
LP	2.9NS	1.7	−13.7***	3.8	11.5***	3.6
MCI1	8.3***	0.1	3.9***	0.3	9.4***	0.3
MCI2	9.6***	0.1	3.7***	0.3	10.3***	0.3
CI	27.9***	3.4	4.7NS	6.9	13.1*	6.9

[a] Data of milk yield recorded in kg; LP and CI in days; MCI1 and MCI2 in kg/day; AC1 in months. NS, non-significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

Table 6. **Estimates of maternal additive effects (G^M) for different traits in the first and all lactations in the three crossing trials**

	Fayoum trial		Gharbia trial		Giza trial	
Trait[a]	Estimate	SE	Estimate	SE	Estimate	SE
First lactation:						
M90	956***	75	395***	87	791***	133
M305	2576***	247	995***	244	2257***	449
TMY	3017***	299	1095***	270	2505***	505
LP	9.1NS	8.0	−3.3NS	8.5	13.7NS	13.2
MCI1	6.5***	0.7	2.7***	0.7	6.8***	1.2
MCI2	7.6***	0.7	3.1***	0.7	7.2***	1.3
CI	13.5NS	17.2	−13.1NS	15.7	−33.6NS	28.2
AC1	−1.9*	0.9	−0.1NS	0.9	0.7NS	1.8
All lactations:						
M90	1125***	17	435***	29	1003***	41
M305	3115***	54	1298***	84	2901***	134
TMY	3656***	61	1326***	93	3159***	146
LP	−4.9*	2.1	−0.1NS	2.9	6.4NS	5.0
MCI1	7.3***	0.2	3.4***	0.2	7.9***	0.4
MCI2	8.5***	0.2	3.5***	0.3	8.4***	0.4
CI	25.6***	4.2	−0.1NS	5.3	8.0NS	9.5

[a] Data of milk yield recorded in kg; LP and CI in days; MCI1 and MCI2 in kg/day; AC1 in months. NS, non-significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

Direct additive effect

For most lactation traits in the three trials, estimates of individual additive effect ($G^I = g^I_H - g^I_F$) were generally large and in favour of H cows (Table 5). These results indicate that H cows are superior ($p < 0.001$) in their direct additive effects for lactation traits over F cows. Such superiority of G^I for milk traits in H cattle was also observed by ROBISON et al. (1981) for H crossed with Brown Swiss and Ayrshire, by MADALENA et al. (1990a) for H crossed with Guzera, by AHLBORN-BREIER and HOHENBOKEN (1991) for H crossed with jersey, and by TOUCHBERRY (1992) for H crossed with Guernsey. For H crossed with Zebu, MARTINEZ et al. (1988) concluded for each 1% of H gene contribution, an increase of 10.02, 12.02, 12.51 and 12.15 kg of milk per lactation was expressed in the first, second, third lactation and all lactations from the first to fifth lactation, respectively.

Estimates of G^I for CI in Fayoum and Giza trials were moderate or highly significant and unfavourable for H cows (Table 5), whereas they were insignificant but in favour of H cows for AC1 in Gharbia and Giza trials, i.e. H cows showed mostly longer (unfavourable) CI and earlier AC1 than F cows. These results are in agreement with those reported by LIN et al. (1984) with H and Ayrshire cattle. MARTINEZ et al. (1988) showed that, on the average, H cows mature 6 months earlier than the Zebu cows and recorded a shorter CI of 37 days ($p < 0.01$) than the latter. TOUCHBERRY (1992) reportred that H recorded a longer CI (by 9.4 days) ($p < 0.05$) and an insignificantly earlier AC1 (0.4 month) than Guernseys.

Maternal additive effect

For M90, M305, TMY, MCI1 and MCI2 in the three trials, estimates of maternal additive effect ($G^M = g^M_H - g^M_F$) were large ($p < 0.001$) and in favour of H dams (Table 6). The estimates for LP in the three trials were insignificant and in favour of F dams. These results indicate that daughters of H dams recorded higher milk production ($p < 0.001$) and shorter LP than daughters of F dams. For H crossed with Ayrshire or Brown Swiss, estimates of G^M cited by ROBISON et al. (1981) and RINCON et al. (1982) evidenced the superiority of H dams in milk-yield traits relative to dams of the other dairy breeds. An opposite trend was observed by AHLBORN-BREIER and HOHENBOKEN (1991) and MCALLISTER et al. (1994) who found that daughters of Jersey or Ayrshire dams recorded higher milk yield than daughters of H dams. In Egypt, ARAFA (1996) reported also that daughters of F dams had higher M90, M305, TMY, MCI1 and MCI2 than daughters of native Domiati dams.

In the three trials, estimates of G^M for CI were positively associated with negative estimates for AC1 and in favour of F dams (Table 6). These findings reveal that additive maternity of effects of H dams showed shorter CI and AC1 than additive maternity effects of F dams. In Canada, LIN et al. (1984) with H × Ayrshire crosses from Canada and USA reported that additive maternity effects of Ayrshire dams showed later AC1 than the additive maternity effects of H dams. THORPE et al. (1993) with F, Sahiwal and their crosses showed that daughters of Sahiwal dams recorded insignificantly longer CI by 18 days than daughters of F dams, whereas AC1 was earlier by 2.27 months in favour of F dams. With native Domiati cattle upgraded with F in Egypt, ARAFA et al. (1998) reported that estimates of G^M for CI and AC1 were in favour of Domiati dams ($p < 0.01$ or $p < 0.001$), i.e. additive maternity effects of F dams showed longer CI and older AC1 than the additive maternity effects of Domiati dams.

Direct heterosis

The estimates of direct heterotic effects (H^I) for M90, M305, TMY, MCI1 and MCI2 in the three trials were mostly negative (Table 7). For all lactations, these estimates ranged from -9.9 to -8.4% in the Fayoum trial, from -0.4 to 0.1% in the Gharbia trial and from -2.2 to 0.5% in Giza trial. The estimates of H^I for milk-yield traits in Fayoum trial were significant ($p < 0.001$), whereas they were mostly insignificant in the Gharbia and Giza

Table 7. **Estimates (in actual units) and percentages of direct heterosis (H^I) for milk and reproductive traits in the three crossing trials**

	Fayoum trial			Gharbia trial			Giza trial		
Trait	Estimate (actual)	SE	(H%)†	Estimate (actual)	SE	(H%)†	Estimate (actual)	SE	(H%)†
First lactation:									
M90	−177.7***	22.4	−9.1	−47.5NS	37.0	−2.5	−40.5NS	69.3	−2.1
M305	−388.6***	74.4	−8.5	−8.5NS	103.5	−0.2	−22.5NS	234.0	−0.5
TMY	−498.4***	90.2	−9.3	−48.3NS	114.6	−1.0	−55.6NS	263.5	−1.1
MCI1	−2.8NS	2.4	−0.8	−3.8NS	3.6	−1.2	−0.8NS	6.9	−0.2
MCI2	−0.95***	0.20	−8.4	−0.13NS	0.29	−1.8	−0.24NS	0.63	−2.1
LP	−1.18***	0.22	−9.1	−0.22NS	0.31	−1.2	−0.17NS	0.69	−1.4
CI	1.2NS	5.2	0.3	4.0NS	6.8	1.1	0.5NS	14.6	0.1
AC1	−0.52*	0.27	1.9	−0.45NS	0.43	−1.6	−0.37NS	0.91	−1.3
All loctations:									
M90	−214.0***	5.3	−9.8	−0.3NS	13.2	−0.1	−46.7**	19.8	−2.2
M305	−509.2***	17.3	−9.5	−9.4NS	38.0	−0.2	−27.9NS	64.3	−0.5
TMY	−619.8***	19.6	−9.9	−24.9NS	42.3	−0.4	27.6NS	70.1	0.5
MCI1	−1.10***	0.05	−8.4	0.01NS	0.11	0.1	−0.14NS	0.18	−1.1
MCI2	−1.32***	0.05	−8.8	−0.03NS	0.11	−0.2	0.01NS	0.19	0.1
LP	2.1**	0.7	0.6	−2.0NS	1.3	−0.6	3.6NS	2.4	1.0
CI	−4.6***	1.4	−1.1	1.1NS	2.4	0.3	1.6NS	4.6	0.4

† H%, [Actual estimates of heterosis/mid-parents] × 100
NS, non-significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

trials. The negative estimates of H^I in the three trials may reveal that crossing H with F in hot climate zones was associated, unfortunately, with a decrease in the performance of the crossbred cows for milk yield traits. The reason for these negative heterosis may be due to that these crossing experiments dealt with crosses between two rather closely related strains of dairy cattle. In temperate zones, negative estimates of H^I were obtained by RINCON et al. (1982) for TMY in the first lactation of H crossed with Ayrshire (−1.3%) and by ZARNECKI et al. (1993) for M305 of the first lactation of Polish F crossed with three H strains from Israel (−2.7%), Sweden (−1.9%) and United Kingdom (−1.2%). In Egypt, crossing and upgrading of native cattle with F in this hot-climate country gave an improvement in the lactational performance of crossbred cows (ARAFA 1996). In other hot-climate countries, MARTINEZ et al. (1988) and MADALENA et al. (1990a) in Brazil and THORPE et al. (1993 and 1994) in Kenya reported that crossing H or F with their native cattle was associated with positive HG^I for milk production. The estimates reported in these papers ranged from 1.6 to 8.6% for M90, from 0.6 to 21.2% for M305, from 3.2 to 16.5% for TMY, from 1.3 to 13.3% for MCI1 and from 1.8 to 11.0% for MCI2.

Estimates of H^I for LP in the Fayoum trial ($p < 0.01$) and the Giza trial ($p > 0.05$) were positive (Table 7). DONALD et al. (1977) for F crossed with Ayrshire, RINCON et al. (1982) for H crossed with Ayrshire or Brown Swiss and MADALENA et al. (1990a) for H crossed with Guzera reported positive H^I for LP.

Negative and significant ($p < 0.001$) estimate of H^I for CI was recorded in the Fayoum trial (Table 7). On the other hand, the estimates of H^I for CI in the Gharbia and Giza trials were positive and insignificant, i.e. crossing F with H in an adverse environment was associated with a slight increase in the CI of crossbred cows. Negative and non-significant estimates of H^{I} for AC1 obtained in the three trials (Table 7) show that crossbred cows had younger AC1 than the average of their purebred parents. Reduction in AC1 or CI was also observed by most of the reviewed studies in crossbreeding trials including H and/or F and their crosses with other breeds (e.g. Donald et al. 1977; Rincon et al. 1982; Lin et al. 1984; Martinez et al. 1988; Madalena et al. 1990a, b; Thorpe et al. 1993; Arafa et al. 1998).

Maternal heterotic effect

The estimates of maternal heterotic effects (H^{M}) for different traits in the Gharbia trial are contradicted by the estimates of the other two trials (Table 8). Across all lactations, the estimates of H^{M} for M90, M305, TMY, MCI1 and MCI2 ranged from −13.5 to −10.6% for the Fayoum trial, from 0.1 to 2.6% for the Gharbia trial and from −5.3 to −3.1% for the Giza trial. In the Fayoum and Giza trials, H^{M} for milk-yield traits were negative ($p < 0.01$ or $p < 0.001$), although they were positive and mostly insignificant in the Gharbia trial. High negative estimates of H^{M} for milk-yield traits indicate that crossbred dams did not show heterotic maternity. Thorpe et al. (1993) found with F crossed with Sahiwal in Kenya that the estimate of H^{M} for TMY was positive and moderate. In Egypt, Arafa (1996) found that for native Domiati cattle crossed with F the estimates of H^{M} for milk-yield traits were positive ($p < 0.01$ or $p < 0.001$); the estimates ranged from 3.7 to 14% for M90, from 7.5 to 17.1% for M305, from 5.6 to 19.6% for TMY, from 13.1 to 21.1% for MCI1 and from 14.1 to 23.3% for MCI2. On the other hand, Ahlborn-Breier and Hohenboken (1991) for H crossed with Jersey and McAllister et al. (1994) for H crossed with Ayrshire reported insignificant negative estimates of H^{M} for TMY.

Table 8. **Estimates of maternal heterosis (H^{M}) for different traits in the first and all lactations in the three crossing trials**

	Fayoum trial			Gharbia trial			Giza trial		
Trait	H^{M} (actual)	SE	H^{M} (%)†	H^{M} (actual)	SE	H^{M} (%)†	H^{M} (actual)	SE	H^{M} (%)†
First lactation:									
M90	−192.2***	39.2	−9.8	24.8NS	58.8	1.3	−24.4NS	112.9	−1.3
M305	−495.9***	129.8	−10.8	−128.0NS	164.6	−2.9	191.2NS	381.3	4.3
TMY	−699.7***	157.5	−13.0	−27.8NS	182.3	−0.6	407.0NS	429.3	7.9
MCI1	−1.71***	0.34	−12.4	−0.42NS	0.46	−3.8	0.67NS	1.03	5.9
MCI2	−1.73***	0.38	−13.2	−0.12NS	0.49	−1.0	1.29NS	1.12	10.1
LP	−15.7**	4.2	−4.5	4.9NS	5.7	1.5	24.0*	11.2	7.0
CI	−18.5*	9.1	−4.6	−18.5NS	10.7	−4.9	20.3NS	23.5	5.4
AC1	−2.63***	0.45	−9.4	1.25*	0.64	4.5	4.67***	1.32	17.0
All lactations:									
M90	−230.7***	9.9	−10.6	33.0NS	18.5	1.6	−110.5***	19.7	−5.3
M305	−633.8***	32.4	−11.8	13.1NS	53.2	0.3	−208.9***	63.8	−4.1
TMY	−846.3***	36.6	−13.5	148.6**	59.2	2.6	−189.1**	69.5	−3.1
MCI1	−1.51***	0.09	−11.6	0.01NS	0.15	0.1	−0.58**	0.18	−4.5
MCI2	−1.94***	0.09	−12.9	0.35*	0.16	2.5	−0.57**	0.18	−3.9
LP	−8.4***	1.3	−2.4	10.8***	1.9	3.3	4.7*	2.4	1.4
CI	−2.7NS	2.6	−0.6	−4.5NS	3.3	−1.2	11.4**	4.5	2.9

H^{M}%, [Actual estimates of maternal heterosis/mid-parent] × 100
NS, non-significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

The estimates of H^M for LP in the Gharbia and Giza trials were positive ($p < 0.05$ or $p < 0.001$), although they were negative ($p < 0.001$) in the Fayoum trial (Table 8). However, a positive estimate of H^M for LP was favourable for cattle producers in developing countries. This indicates that crossbred dams recorded longer lengths of LP in their crossbred daughters than in their purebred dams. Results obtained in the Gharbia and Giza trials agree well with those obtained by ARAFA (1996) for upgrading trial of native Domiati with F in Egypt. THORPE et al. (1993) in Kenya reported also that the estimate of H^M for LP was insignificantly positive.

The estimates of H^M for CI and AC1 were mostly significant in the three trials (Table 8). The estimates in the three trials are contradictory and ranged from −9.4 to 17.0%. Findings reveal generally that the daughters of crossbred dams recorded shorter lengths of CI and earlier AC1 than daughters of the purebred dams. Similarly, THORPE et al. (1993) with Sahiwal crossed with F and Ayrshire in Kenya recorded insignificant negative estimates of H^M for CI and AC1. In Egypt, ARAFA et al. (1998) with three upgrading trials of native Domiati cattle with F, Shorthorn and Jersey reported positive H^M for CI.

Direct recombination effect

The estimates of direct recombination loss (R^I) for M90, M305, TMY, MCI1 and MCI2 in the three trials were negative and significant (Table 9). However, the significant effect of R^I indicates that there would be a considerable difference in heterosis as measured and expected in a particular cross. The negative estimates of R^I in all lactations ranged from −88.2 to −10.7 kg for M90, from −239.7 to −47.4 kg for M305, from −305.0 to −29.1 kg for TMY, from −0.54 to −0.13 kg for MCI1 and from −0.68 to −0.08 kg for MCI2 (Table 9). Negative and significant R^I for milk-yield traits reveal that crossbred cows with H blood could mother heifers with lower milking ability than purebred H cows when both groups

Table 9. **Estimates of individual recombination effects (R^I) for different traits in the first and all lactations in the three crossing trials**

	Fayoum trial		Gharbia trial		Giza trial	
Trial	Estimate	SE	Estimate	SE	Estimate	SE
First lactation:						
M90	−69.9***	9.7	−20.7NS	13.9	−42.4NS	25.6
M305	−182.7***	32.1	−83.1*	29.0	−69.9NS	86.4
TMY	−240.6***	38.9	−65.6NS	43.1	−35.4NS	97.3
MCI1	−0.47***	0.09	−0.21*	0.11	−0.21NS	0.23
MCI2	−0.59***	0.09	−0.17NS	0.12	−0.13NS	0.25
LP	−3.6**	1.0	−0.2NS	1.4	4.1NS	2.5
CI	−4.0NS	2.3	−3.6NS	2.5	12.8**	5.2
AC1	−0.54***	0.11	−0.25NS	0.15	0.98**	0.34
All lactations						
M90	−88.2***	2.2	−10.7*	4.6	−71.2***	5.7
M305	−239.7***	7.2	−47.4***	13.4	−180***	18.6
TMY	−305.0***	8.1	−29.1*	14.9	−190***	20.3
MCI1	−0.54***	0.02	−0.13***	0.04	−0.50***	0.05
MCI2	−0.68***	0.02	−0.08*	0.04	−0.53***	0.05
LP	−1.3***	0.3	1.5***	0.5	0.7NS	0.7
CI	−0.5NS	0.6	−0.7NS	0.8	3.9**	1.3

NS, non-significant; $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

of cows were mated to bulls from the same purebred H. Similarly, negative ($p < 0.05$) estimates of R^I for M305 were reported by PEDERSEN and CHRISTENSEN (1989) with Finnish Ayrshire, Red Danish, H, Danish F and their crosses. VAN DER WERF and DE BOER (1989a) for H crossed with Dutch F, and AKBAS et al. (1993) and BOICHARD et al. (1993) for H crossed with European Black and White cattle reported also that estimates of R^I for M305 and/or TMY were insignificantly negative. ARAFA (1996) for three upgrading trials of Domiati cattle with F, Shorthorn and Jersey in Egypt found that estimates of R^I for M90, M305, TMY, MCI1 and MCI2 were mostly positive and significant.

In the Fayoum trial, estimate of R^I for LP was negative ($p < 0.001$), whereas it was positive in the Gharbia and Giza trials (Table 9). The results of the Fayoum trial are contradicted by those of the other two. This may be due to differences in the number of animals used in these trials. ARAFA (1996) in Egypt reported positive estimates of R^I for LP in the first separate lactations ($p < 0.01$ or ($p < 0.001$) through crossing of F with native Domiati cattle.

Negative estimates of R^I for CI and AC1 were recorded in Fayoum and Gharbia, whereas they were positive ($p < 0.01$) in Giza (Table 9). ARAFA et al. (1998) in Egypt using native Domiati cattle upgraded with **F** or Shorthorn or Jersey found that estimates of RI for CI and/or AC1 were generally positive and insignificant.

VAN DER WERF and DE BOER (1989a, b) pointed out that in the two locus model heterosis reflects dominance and half the additive by additive interaction effects whereas the recombination effect consiss of half the additive by additive interaction effects. In comparisons of R^I estimates with those of H^I in the present work, the negative estimates of H^I for milk-yield traits in Gharbia and Giza trials were generally larger than estimates of R^I, whereas the reverse was true in the Fayoum trial (Tables 7 and 9). PEDERSEN and CHRISTENSEN (1989), VAN DER WERF and DE BOER (1989a) and BOICHARD et al. (1993) concluded that estimates of R^I for M305 and/or TMY were negative and smaller than those estimates of H^I. For LP, CI and AC1, contradicting estimates of R^I in the three trials were observed. Results in the Gharbia and Giza trials agreed with ARAFA (1996) and ARAFA et al. (1998) in Egypt for native Domiati cattle crossed with F and Shorthorn. They reported that estimates of R^I for M305, TMY, MCI1, MCI2, LP and CI were generally larger than those estimates of heterosis, which also implies that the dominance effects on these traits were negative in most cases.

Conclusion

(1) Under hot-climate conditions, the superiority of direct and maternal additivity of the Holstein breed over Friesian for most lactation and reproductive traits indicates that Holstein could be used as an effective breed in the dairy industry in Egypt to improve these traits through crossing of Holstein with native breeds.

(2) Since estimates of direct and maternal heterosis obtained in the present study were negative for most traits, it is not advisable to cross Holstein with Friesian in an adverse environment such as a hot climate.

(3) The significant negative recombination effects on milk-yield traits were unfavourable and indicate that epistatic recombination losses for these traits were of considerable importance. Therefore, there is no advantage in using crossbred dams that result from crossing Holsteins with Friesians to develop parental strains to be used in crossbreeding stratification in hot-climate regions (particularly in Egypt).

(4) In the three trials of these commercial herds, since maternal additivity for milk-yield traits were most positive, therefore, it is preferable to use crossbred cows resulting from purebred dams instead of using crossbred cows from crossbred dams.

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Authors' addresses: M. H. Khalil, Department of Animal Production & Breeding, College of Agriculture & Veterinary Medicine, King Saud University, Buriedah P.O. Box 1482, Saudi Arabia; E. A. Afifi and M. A. Salem, Department of Animal Production, Faculty of Agriculture at Moshtohor, Zagazig University, Egypt; S. M. Zahed, Animal Production Research Institute, Ministry of Agriculture, Dokki, Egypt.