January 1984

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ABSTRACT

Inbreeding coefficients of artificially bred Ayrshire, Guernsey, Holstein, Jersey, and Brown Swiss cows were calculated from relationships between sires and maternal male ancestors. Percentages of inbred cows and average inbreeding coefficients of inbred cows were: Ayrshire, 26 and 11%; Guernsey, 11 and 4%; Holstein, 31 and 1%; Jersey 23 and 2%; and Brown Swiss, 23 and 2%. Percentages of inbred cows and average inbreeding coefficients of all cows increased over time whereas average coefficients of inbred cows decreased over time. These temporal trends may be due in part to having more pedigree information available for cows born in later years. Effects of inbreeding on milk and fat yields of first lactation (2 times milked, 305-day mature equivalent), 48-mo stayability, and first calving interval were estimated with a model including effects for fixed herd-year-seasons, fixed sire and maternal grandsire groups, random sires and maternal grandsires within groups, and random residual. Regression coefficients of milk (kg), fat (kg), 48-mo stayability (proportion of cows surviving to 48 mo of age), and calving interval (days) on inbreeding coefficient (%) were: Ayrshire −27.1, −1.2, −.005, .23; Guernsey −19.3, −.97, −.007, .27; Holstein −21.1, −.78, −.003, .09; Jersey −14.8, −.80, −.002, .63; and Brown Swiss −39.5, −1.36; −.011, .03. There is no cause for concern over current inbreeding, but active inbreeding is not recommended.

Received November 12, 1982.

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INTRODUCTION

Modern artificially bred (AI) dairy populations are characterized by only a few bulls servicing many females. Outstanding bulls often have numerous female descendents, and the same bulls are likely to sire many sons that eventually enter AI service. If inbreeding is to be avoided, breeding opportunities may be limited if available bulls are closely related to a large proportion of the female population. Hudson and Van Vleck (10) reported amount and effects of inbreeding on production, stayability, and calving interval of registered Ayrshire cattle. This paper documents inbreeding of AI cattle (registered and nonregistered) of the Ayrshire, Guernsey, Holstein, Jersey, and Brown Swiss breeds. Effects of inbreeding on milk and fat yields of first lactation, 48-mo stayability (proportion of cows surviving to 48-mo of age), and first calving interval also were estimated.

MATERIALS AND METHODS

Inbreeding coefficients were calculated for all artificially bred Ayrshire, Guernsey, Holstein, Jersey, and Brown Swiss cows identified on files of the New York Dairy Records Processing Laboratory (DRPL) by methods described by Hudson and Van Vleck (10). A partial pedigree including sire of cow and up to seven male ancestors of dam of cows was built for each cow. Relationships among males were calculated by the tabular method (8), and the inbreeding coefficient of each cow was estimated as a function of relationships between sire and maternal male ancestors (10). Cow pedigrees were built with only AI bulls to reduce the size of the relationship matrix calculated. Thus, for example, a cow with a non-AI dam but with an AI maternal granddam would have only a partial inbreeding coefficient.

First lactation, 2 ×, 305-day, mature equivalent (ME) milk and fat records, calving dates, and stayability information were obtained from DRPL files and subjected to edits described in (10). Characteristics of the data sets are in Table 1.

The basic model was the sire-maternal grandsire model (4, 12):

$$y_{ijkmnp} = h_i + g_j + s_{jk} + .5\,(g'_m + s'_{mn}) + e_{ijkmnp}$$

where

y_{ijkmnp} = record of the p^{th} cow in the i^{th} herd-year-season with sire k of the j^{th} group and with maternal grandsire n of the m^{th} group;
h_i = fixed effect of the i^{th} herd-year-season,
g_j = fixed effect of the j^{th} sire group,
s_{jk} = random effect of the k^{th} sire in the j^{th} group with mean 0 and variance σ_s^2,
g'_m = fixed effect of the m^{th} maternal grandsire group,
s'_{mn} = random effect of the n^{th} maternal grandsire in the m^{th} group with mean 0 and variance σ_s^2, and
e_{ijkmnp} = residual associated with the $ijkmnp^{th}$ record with mean 0 and variance σ_e^2.

Inbreeding was included in the model either as a classification variable [six classes for cows with known inbreeding coefficients (F): F = 0, $0 < F < 5\%$, $5 \leqslant F < 10\%$, $10 \leqslant F < 15\%$, $15 \leqslant F < 25\%$, and $F \geqslant 25\%$; and one class for cows with indeterminate inbreeding coefficients] or as a linear covariate. Further details of the model are in (10). Year-seasons and sire groups were defined as in (10) except that Holstein group size was 100 whereas group size for other breeds was 25. Heritabilities used in the mixed model equations are in Table 2.

RESULTS AND DISCUSSION

Inbreeding

Table 3 shows inbreeding coefficients of bulls calculated from the diagonals of the relationship matrix for AI sires. A higher proportion of Holstein bulls were inbred than were bulls of the other breeds, but the average inbreeding of inbred bulls was lowest for Holsteins. Ayrshires had the highest average inbreeding coefficient of all bulls. Ayrshire bulls in (10) included all bulls (natural service and AI); this study included only AI bulls. A higher proportion of AI bulls than of all bulls were inbred (4.7 vs. 1.8%), and the average inbreeding coefficient of AI bulls was higher than that of all bulls (.39 vs. .13%). Watson (14) found AI Welsh Black bulls were more inbred than natural service bulls (2.8 vs. 2.2%) whereas O'Connor and Willis (11) found the opposite; AI British Friesian bulls were less inbred than natural service sires (1.30 vs. 2.08%). Both studies (11, 14) sampled herd books for 1 yr only.

The percent inbred Holstein bulls was nearly double the 6.3% of British Friesians from 1955 to 1972 (3). However, average inbreeding of the Holstein bulls was less than of the Friesians. The average inbreeding of inbred Friesian bulls was 7.4% and of all bulls .46% (3).

A higher proportion of Holstein cows were inbred than were cows of the other breeds (Table 4). However, the average inbreeding coefficient of inbred cows was lowest for Holsteins. Average inbreeding coefficient of inbred Ayrshire cows was higher than that of

TABLE 1. Number of sires and maternal grandsire (mgs), cows, and herds in each data set.

	Ayrshire	Guernsey	Holstein	Jersey	Brown Swiss
No. sires and mgs	266	850	5,294	819	266
No. ancestor bulls	93	322	1,234	246	125
Total no. cows	50,688	61,773	1,474,995	81,639	18,516
No. cows with records	27,991	38,021	1,001,392	54,258	10,339
No. herds	1,675	2,148	19,652	2,791	911

other breeds, and the average inbreeding coefficient of all Ayrshires (excluding those with indeterminate inbreeding) was 1.6%, whereas for other breeds average overall inbreeding was less than .5%.

Hudson and Van Vleck (10) reported 17% of registered Ayrshire cows were inbred, less than in Table 4 for AI Ayrshires. There was overlap of the two data sets, i.e., some registered cows were AI; however, the registered data included some non-AI cows, and the AI data set included some nonregistered cattle. Whether the difference of inbreeding in the two data sets is due to AI vs. non-AI or grade vs. registered is unknown. Inbreeding of registered Welsh Black (14) and registered British Friesian (11) was higher for natural service cows than for AI cows. If that is true in the Northeast US Ayrshires, then grade cattle must be substantially more inbred than registered cattle.

Table 5 compares inbreeding of Holsteins of this study with inbreeding of other "black and white" sub-breeds. A larger proportion of cows were inbred in this study, but average inbreed-

TABLE 2. Assumed heritabilities used in the mixed model equations.[1]

	Ayrshire	Guernsey	Holstein	Jersey	Brown Swiss
Milk	.4280	.1952	.3267	.3510	.2750
Fat	.4483	.2032	.3050	.2548	.1976
Stayability	.0237	.0977	.0256	.0812	.1583
Calving interval	.01	.01	.01	.01	.01

[1] Estimates for milk, fat, and stayability from Hudson and Van Vleck (9); estimate for calving interval from Foote (5).

TABLE 3. Inbreeding of artificial insemination (AI) bulls.

	Ayrshire	Guernsey	Holstein	Jersey	Brown Swiss
No. of bulls	359	1172	6528	1065	391
No. inbred bulls[1]	17 (4.7)	33 (2.8)	792 (12.1)	42 (3.9)	30 (7.6)
Avg. inbreeding (%)					
All bulls	.39	.17	.36	.14	.26
Inbred bulls	8.30	5.99	2.97	3.61	3.44
Max. inbreeding	12.50	12.50	28.13	12.50	25.00

[1] Figure in parentheses is no. inbred bulls as percent of total no. bulls.

TABLE 4. Numbers of cows and inbreeding (F) by breed.

	Ayrshire	Guernsey	Holstein	Jersey	Brown Swiss
Total no. of cows	50,688	61,773	1,474,995	81,639	18,516
% Cows with known F[1]	71 (76)	63 (72)	77 (74)	68 (77)	67 (75)
% Cows inbred[1]	26 (28)	11 (12)	31 (32)	23 (18)	23 (25)
Avg. F of inbred cows (%)[1]	6 (5)	4 (3)	1 (1)	2 (3)	2 (2)
Max. F (%)	29.7	26.9	49.8	27.2	27.2

[1] Figure in parentheses refers to cows with data.

TABLE 5. Comparison of inbreeding of US Holstein, Canadian Holstein and British Friesian cattle.

Cattle type	Location of cattle	No. of cattle	% Inbred	Avg. inbreeding (%)		Source
				Inbred cattle	All cattle	
US Holstein	NE US	1,002,997	31	1	.3	Present study
	NE US	17,490	7.4	4.9	.4	Allaire and Henderson (1)
	All US	250	. . .	. . .	3.8	Bonczek and Young (2)
	All US	606	. . .	. . .	5.0	Young (16)
Canadian Holstein	British Columbia	728	8.1	6.1	.5	Hodges et al. (6)
		450	9.8	6.0	.6	
British Friesian	United Kingdom	500	23	11.8	2.7	Bowman et al. (3)

ing was lower than in other reports. The sample of Allaire and Henderson (1) was taken from the same DRPL files as was the data set of this study so the discrepancy of those results is the most surprising. However, their procedure (1) underestimated the percent of cows inbred and overestimated the average inbreeding of inbred cows because:

1) only sire-maternal grandsire relationships were used to calculate inbreeding, thus ignoring inbreeding from related ancestors in more distant generations,

2) only daughters of 200 bulls were used, and any maternal grandsire had to be one of those bulls to contribute to inbreeding, and

3) relationships among bulls were calculated from two generation pedigrees. With this procedure, only 4.4% of total possible pairs of bulls were related. In contrast, Van Vleck and Hudson (13) reported 21.8% nonzero off-diagonals in a relationship matrix for 4084 Holstein bulls. Allaire and Henderson (1) thus only accounted for major sources of inbreeding and ignored low inbreeding caused by distant relationships.

Hodges et al. (6) built four-generation cow pedigrees to calculate inbreeding. They ignored inbreeding from common ancestors in the fifth generation, correctly claiming that a common ancestor in that generation adds only .8% to the inbreeding coefficient and that the chance of a common ancestor appearing in the fifth generation and in a later generation is low because of contemporaneity. Hodges et al. (6) also ignored inbreeding of common ancestors. Although differences between Holsteins in the Northeast US and in British Columbia may be real, procedures of this study identified cows with low inbreeding, whereas those cows would have been assumed noninbred by Hodges et al. (6).

The other studies in Table 5 used Wright's (15) short method to estimate inbreeding. Average inbreeding was five times as much as in reports not using Wright's short method. Young (16) sampled registered cows born in 1970, and Bonzcek and Young (2) sampled cows born in 1976. Average inbreeding of cows born in those years in this study was .31 and .38%. The most probable cause of the difference between results reported here and findings of Young and coworkers is the base date used in calculating inbreeding coefficients. Young's studies used a

TABLE 6. Distribution of cows by inbreeding: all cows.[1,2]

Inbreeding (%)	Ayrshire	Guernsey	Holstein	Jersey	Brown Swiss
0	26,477 (73.4)	34,489 (88.7)	697,340 (61.4)	46,078 (82.7)	9,642 (77.2)
0+ – 5−	4,671 (13.0)	3,297 (8.5)	291,503 (25.7)	8,294 (14.9)	2,465 (19.7)
5 – 10−	3,430 (9.5)	721 (1.9)	142,202 (12.5)	846 (1.5)	255 (2.0)
10 – 15−	1,202 (3.3)	273 (.7)	2,652 (.2)	375 (.7)	91 (.7)
15 – 20−	55 (.2)	9 (0)	86 (0)	11 (0)	2 (0)
20 – 25−	3 (0)	0	0	0	0
25 – 30−	79 (.2)	94 (.2)	1,843 (.2)	135 (.2)	33 (.3)
30 – 35−	0	0	7 (0)	2 (0)	0
35 – 40−	0	0	5 (0)	2 (0)	0
40 – 50−	0	0	7 (0)	6 (0)	0
TOTAL	35,917	38,883	1,135,645	55,749	12,488

[1] Excludes cows with indeterminate inbreeding.

[2] Figures in parentheses are percentages of total cows with known inbreeding coefficients.

TABLE 7. Distribution of cows by inbreeding: only cows with data.[1,2]

Inbreeding (%)	Ayrshire	Guernsey	Holstein	Jersey	Brown Swiss
0	15,733 (72.2)	24,180 (87.9)	500,305 (67.6)	34,004 (81.5)	5,805 (75.2)
0+ – 5−	3,121 (14.3)	2,529 (9.2)	226,460 (30.6)	6,626 (15.9)	1,666 (21.6)
5 – 10−	2,189 (10.0)	521 (1.9)	10,453 (1.4)	673 (1.6)	171 (2.2)
10 – 15−	677 (3.1)	194 (.7)	1,927 (.3)	293 (.7)	56 (.7)
15 – 20−	35 (.2)	8 (0)	68 (0)	9 (0)	1 (0)
20 – 25−	1 (0)	0	0	0	0
25 – 30−	48 (.2)	61 (.2)	1,312 (.2)	97 (.2)	19 (.2)
30 – 35−	0	0	5 (0)	1 (0)	0
35 – 40−	0	0	3 (0)	1 (0)	0
40 – 50−	0	0	2 (0)	4 (0)	0
TOTAL	21,804	27,493	740,535	41,708	7,718

[1] Excludes cows with indeterminate inbreeding.

[2] Figures in parentheses are percentages of total cows with known inbreeding coefficients.

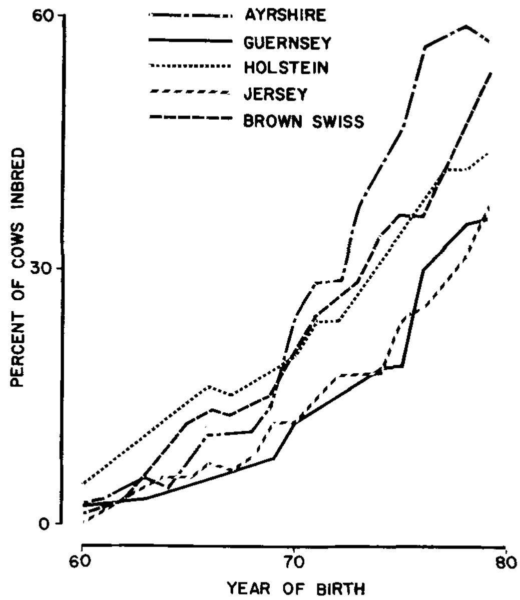

Figure 1. Percent of inbred cows by year of birth.

base date of 1880 whereas the data obtained from DRPL have built up since about 1954.

The majority of inbred cows had inbreeding coefficients less than 15% (Table 6). Percents of inbred cows with inbreeding coefficients 15% or greater in each breed were Ayrshire 1.5, Guernsey 2.3, Holstein .6, Jersey 1.6, and Brown Swiss .9%. Table 7 is similar to Table 6 and indicates the distribution of inbreeding coefficients for cows with data was similar to that for all cows. Tables 4, 6, and 7 present average inbreeding regardless of year of birth. Figure 1 shows the increase of percent inbred cows by year of birth from 1960 to 1979. Fewer than 5% of cows born prior to 1960 were inbred, but this result may be due to lack of pedigree information. The most dramatic increase of percent inbred cows was for the Ayrshire breed from 1972 (28.9%) to 1976 (56.7%). However, Figure 1 indicates that the percent of inbred cows born in 1976 to 1979 has reached a plateau. Although the percent cows inbred has increased dramatically, the average inbreeding coefficient of inbred cows has been decreasing, thus moderating the increase of average inbreeding of all cows (Figures 2, 3, and 4). Average inbreeding has been less than 3% for inbred cows born since 1973 in all breeds (except Ayrshires), and average inbreeding of all cows has never been higher than 1% (Figures 3 and 4). The decrease of inbreeding of inbred Ayrshires (Figure 2) was less than of other breeds (Figure 3). However, the decline of percent inbred Ayrshire cows (Figure 1) and of inbreeding of inbred cows (Figure 2) has resulted in a decrease of inbreeding of all cows since 1976 (Figure 2), whereas average inbreeding of other breeds increased (Figure 4). Although inbreeding of

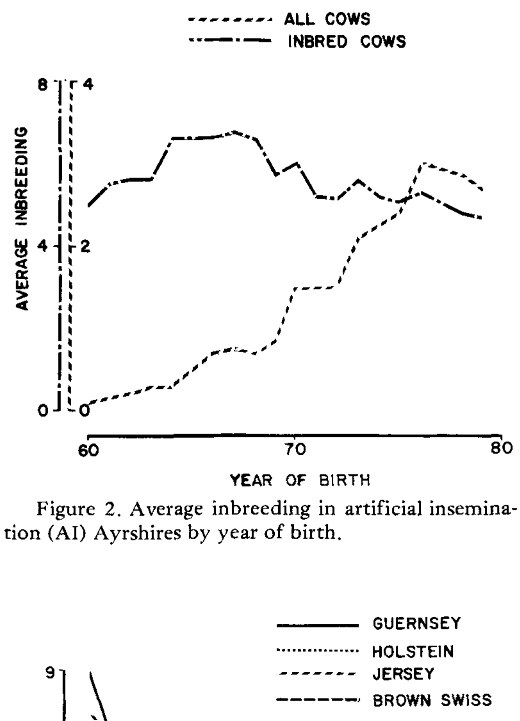

Figure 2. Average inbreeding in artificial insemination (AI) Ayrshires by year of birth.

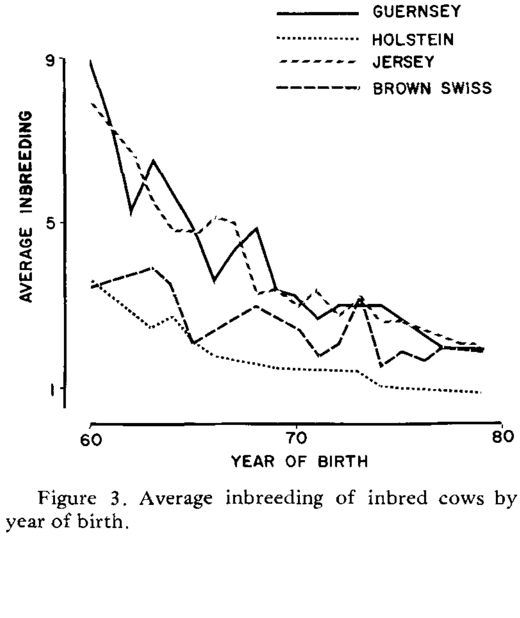

Figure 3. Average inbreeding of inbred cows by year of birth.

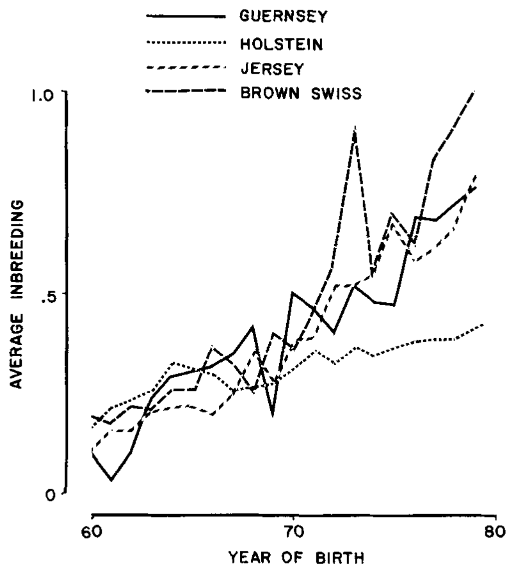

Figure 4. Average inbreeding of all cows by year of birth.

Ayrshires is higher than of other breeds, it is not of such magnitude to cause alarm.

To determine how much inbreeding was intentional and how much was passive, average inbreeding by herd was calculated (Table 8). In all breeds except Holstein, over 60% of herds had no inbred cows; 36% of Holstein herds had inbred cows. However, the average inbreeding in the majority of herds was less than 5%, and fewer than 1% of all herds in each breed had average inbreeding greater than 10%; in no herd was average inbreeding greater than 25%. Similarly, a small proportion of sires had daughters with average inbreeding greater than 5% (Table 9).

Effect of Inbreeding

Table 10 shows estimates of differences for four traits between each of five inbreeding classes and the zero inbreeding class. The 15 to 25% class contained only one Brown Swiss record (Table 7) and was not estimated. For all breeds, the last two classes had few records.

Inbred cattle in all breeds produced less milk and fat than cows that were not inbred. Inbreeding depression increased as inbreeding increased up to 15% for all breeds except Brown Swiss. For Brown Swiss, the estimate for milk for the 10 to 15% class was higher than that for the 0 to 5% class but was lower (absolute) than the associated standard error.

The effect of inbreeding on stayability was

TABLE 8. Distribution of herds by average inbreeding.

Avg. inbreeding (%)	Ayrshire	Guernsey	Holstein	Jersey	Brown Swiss
0	1,016	1,612	7,040	1,864	598
$0^+ - 5^-$	590	520	12,579	908	306
$5 - 10^-$	59	8	21	13	4
$10 - 25^-$	10	8	12	6	3
Total	1,675	2,148	19,652	2,791	911

TABLE 9. Distribution of sires by average daughter inbreeding.

Avg. F (%)	Ayrshire	Guernsey	Holstein	Jersey	Brown Swiss
0	94	327	1,290	269	90
$0^+ - 5^-$	98	246	3,230	345	123
5^+	5	3	10	2	2
Total	197	576	4,530	616	215

TABLE 10. Estimated differences (standard errors) of milk and fat production (kg), stayability (stay; pts), and calving interval (CI; days) between five classes of inbred cows and noninbred cows: all breeds.

		Inbreeding class				
Breed	Trait	0⁺ – 5⁻%	5 – 10⁻%	10 – 15⁻%	15 – 25⁻%	25% +
Ayrshire	Milk	−62.1 (25.2)	−195.1 (28.8)	−353.4 (36.4)	−222.8 (186.0)	−321.6 (166.3)
	Fat	−3.3 (1.0)	−8.4 (1.2)	−15.8 (1.9)	−5.4 (7.4)	−18.6 (6.7)
	Stay	−.02 (.03)	−.03 (.03)	−.09 (.05)	+.05 (.20)	−.08 (.19)
	CI	2.9 (1.8)	.3 (2.0)	3.8 (3.2)	11.6 (11.6)	1.6 (10.7)
Guernsey	Milk	−24.6 (21.6)	−88.5 (42.8)	−289.9 (68.9)	−823.0 (318.2)	−256.8 (146.2)
	Fat	−2.1 (1.0)	−5.4 (2.0)	−14.7 (3.3)	−37.0 (15.1)	−7.9 (6.9)
	Stay	.00 (.02)	−.05 (.03)	−.13 (.06)	−.05 (.26)	−.09 (.12)
	CI	3.5 (1.7)	7.9 (3.5)	3.4 (5.8)	−15.79 (31.7)	−19.2 (10.7)
Holstein	Milk	−10.5 (3.6)	−160.3 (13.0)	−343.7 (29.9)	−381.8 (158.6)	−322.0 (36.4)
	Fat	−.3 (.1)	−5.5 (.5)	−12.8 (1.1)	−19.4 (5.7)	−12.5 (1.3)
	Stay	−.01 (.00)	−.02 (.00)	−.04 (.01)	−.056 (.06)	−.06 (.01)
	CI	.03 (.19)	2.25 (.69)	1.48 (1.63)	−1.93 (9.07)	−.47 (1.99)
Jersey	Milk	−15.5 (13.4)	−84.9 (36.6)	−243.1 (55.1)	−571.0 (295.8)	−126.5 (98.3)
	Fat	−1.1 (.6)	−4.2 (1.8)	−11.8 (2.7)	−31.7 (14.3)	−10.4 (4.8)
	Stay	.01 (.01)	−.04 (.02)	.01 (.03)	.22 (.16)	−.14 (.05)
	CI	.73 (.97)	4.8 (2.7)	3.5 (4.1)	23.2 (20.2)	6.9 (7.4)
Brown Swiss	Milk	−162.2 (45.0)	−323.0 (120.3)	−161.4 (209.1)	... ...	−744. (461.2)
	Fat	−6.5 (1.9)	−10.4 (5.0)	−9.8 (8.7)	... ...	−27.7 (1.9)
	Stay	−.01 (.02)	−.08 (.04)	−.00 (.08)	... ...	−.25 (.02)
	CI	−1.6 (2.7)	6.1 (8.0)	6.24 (12.8)	... ...	−17.5 (2.77)

TABLE 11. Regression coefficients (standard errors) of milk and fat production (kg), stayability (pts), and calving interval (days) on inbreeding.

	Ayrshire		Guernsey		Holstein		Jersey		Brown Swiss	
Milk	−27.1	(3.5)	−19.3	(3.9)	−21.2	(1.2)	−14.8	(2.9)	−39.5	(10.6)
Fat	−1.2	(.12)	−.97	(.18)	−.78	(.04)	−.80	(.14)	−1.36	(.44)
Stayability	−.005	(.002)	−.007	(.002)	−.003	(.001)	−.002	(.002)	−.011	(.004)
Calving interval	.23	(.22)	.27	(.29)	.09	(.01)	.63	(.04)	.03	(.88)

small in all breeds, and most of the estimates were similar to their standard errors, indicating that inbreeding does not affect adversely the longevity of a cow once first calving has been reached. Hudson and Van Vleck (10) suggested that animals with reduced livability because of intense inbreeding did not appear in the data. Inbreeding has affected pre- and postnatal mortality and disposals prior to first calving (17), but in this study cows had to initiate a first lactation to appear in the data.

If cows with high inbreeding coefficients died or were culled for reproductive reasons prior to initiation of first lactation, then those cows were not in this study. Effects of inbreeding on milk and fat production are probably minimum estimates, because cows with high inbreeding coefficients that did not appear in the data may have had lower milk and fat yields than cows with high calculated coefficients that did appear in the data.

A review of the North Central cooperative project (17) reported that inbred cows had reduced reproductive performance compared to outbreds. Cattle with a measured calving interval are proven reproducers; i.e., they must have had two calvings to have a calving interval. Thus, the lack of effect of inbreeding on calving interval (Table 10) may have been dependent on the data.

The regression of milk on inbreeding coefficient ranged from −15 kg for Jersey to −40 kg per 1% increase of inbreeding for Brown Swiss (Table 11). The range of regression of fat on inbreeding was −.8 kg (Holstein) to −1.4 kg (Brown Swiss). Regressions for both milk and fat were within the range in the literature for all breeds (7). The lack of effect of inbreeding on stayability and calving interval is also suggested by the small, mostly nonsignificant regressions in Table 11.

CONCLUSIONS

A small proportion of cows were inbred. The average inbreeding coefficients of inbred cows and of all cows were low. Although the percent of inbred cows has increased over time, the average inbreeding coefficient of inbred cows has decreased. Inbreeding was more extensive in Ayrshire cattle than in cattle of other breeds; but average inbreeding was low, and there was evidence that the percent of inbred cows has been decreasing since 1976. Whether inbreeding will become more prevalent in the future is not known, but relationships among sires do not indicate that inbreeding will decrease.

Production of milk and fat in first lactation decreased as inbreeding coefficients increased, but inbreeding depression was not enough to cause large reduction of milk yield of a cow with average inbreeding. However, inbreeding depression was such that intentional inbreeding is not justified unless the inbreeding is to an animal with exceptionally high breeding value. Thus, there is no cause for concern over current passive inbreeding, but active inbreeding is not recommended.

In these data, there was no effect of inbreeding on 48-mo stayability or on first calving interval given that the cow survived to freshen a first time.

ACKNOWLEDGMENTS

This research was supported in part by a grant from Eastern Artificial Insemination Cooperative, Inc., Ithaca, NY.

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