

ESTIMATES OF HERITABILITY AND CORRELATION OF FLY SUSCEPTIBILITY
WITH VARIOUS CHARACTERISTICS OF DAIRY CATTLE

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PREFACE

The variation of fly susceptibility in dairy cattle was brought to the attention of the author by Dr. D. E. Howell, Head of the Department of Entomology. Since no extensive study of the cause of this variation could be found in the literature, the author selected as a thesis problem a study of the heritability of this trait and its phenotypic correlation with certain physical characteristics of dairy cattle.

Although the limited amount of data available for a study of this nature makes definite conclusions unjustified, the author believes that it will serve as an indicator to the entomological investigator and animal breeder.

The author wishes to express his appreciation to his major advisor, Dr. D. E. Howell, for his thoughtful guidance and encouragement throughout the study and in the preparation of this paper. Also, sincere thanks are expressed to Dr. E. R. Berousek, Associate Professor of Dairy Production, for his valuable assistance and guidance in planning the research and constructing the thesis; to Dr. Robert D. Morrison, Associate Professor of Mathematics, for assistance in planning the statistical analyses and for helpful suggestions in the preparation of this paper; to Dr. W. A. Drew, Assistant Professor of Entomology, and Mr. G. A. Bieberdorf, Assistant Professor of Entomology, for their constructive criticism of the thesis manuscript.

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INTRODUCTION

The ability of domestic animals to cope with their environment is somewhat dependent upon their biological fitness. Therefore, the desirability and feasibility of breeding animals that perform better than their ancestors under similar environmental conditions becomes obvious.

This study is primarily concerned with the amount of progress that might be expected in breeding dairy cattle for lowered susceptibility to various species of flies. Several investigators (Pearson et al., 1933; Fryer, et al., 1943; and Pearson, 1935) working with fly repellents and insecticides on dairy cattle have concluded that one of the primary reasons for large variations in results is due to individual fly susceptibility. These workers have also recognized the importance of attempting to balance groups of cows for fly susceptibility by making pre-treatment fly counts. In this case, it would seem that an increased knowledge of the factors which are thought to influence fly susceptibility could be of benefit in evaluating those effects due to chemicals and those due to variations among test animals.

The breeding of dairy cattle for lowered fly susceptibility becomes even more desirable when the problems encountered in the use of chemical compounds are considered. The excretion of these materials and their breakdown products in milk and the growing problem of insecticide resistance in insects have definitely limited the use of chemical materials for control purposes. Also, it cannot be overlooked that control

brought about by inheritance would be of a more permanent nature than that afforded by chemical means. If the resemblance in fly susceptibility between individual cows is largely due to genetic relationship, then it would be possible to develop cattle that are less susceptible to flies. By measuring the differences between cows of known relationship, the animal breeding investigator has devised means of estimating that portion of the difference that is due to inheritance. This value is called "heritability."

Thus, the objectives of this study are to correlate fly susceptibility with certain phenotypic characteristics of the dairy cow and to estimate "heritability" of the same. The results should be of interest to the animal breeder, as well as, the entomological investigator.

REVIEW OF LITERATURE

The variation of dairy cattle susceptibility to various species of flies was pointed out by Pearson et al. (1933). He indicated the importance of determining individual fly susceptibility for dairy cows to be used in the testing of fly sprays. Pearson et al. also suggested the determination of normal fly susceptibility by making hourly fly counts from seven a.m. to three p.m. for a period of three days. While conducting repellent tests on dairy cattle, Fryer et al. (1943) concluded that one of the large variations in counts of the stable fly, Stomoxys calcitrans (Linn.) was due to cow-to-cow differences in susceptibility.

An attempt to correlate fly susceptibility with phenotypic characteristics of dairy cattle was made by Pearson (1935). He had little success in trying to correlate susceptibility with such factors as age, color, size, and period of lactation. However, Marlatt (1910) noted the preference of the horn fly, Siphona irritans (Linn), for dark colored cattle. He observed that dark colored cattle were usually more heavily infested with horn flies than light colored cattle. Smith (1889), in one of the early investigations of the horn fly in the United States, observed that the difference in reactions of dairy cows to attack by this pest was due to variation in the thickness of the skin of individual cows. He stated that the thicker skinned cows were less susceptible to fly attack.

No color preference studies with the house fly, Musca domestica Linn., on cattle were found; however, tests have been made which indicate

that the house fly prefers dark to light colors when identical physical surfaces are involved (Freeborn and Berry, 1935; and Harsham, 1946). Mayne (1913) and West (1951) have reported house flies feeding on blood droplets in close association with the stable fly even though the house fly is not commonly associated with the facultative haematophagous types. If this association is highly prevalent it would indicate a possible relationship between the numbers of these species found on individual cows. Also, Mayne concluded that sick animals are more susceptible to attacks by the stable fly because of the fact that this fly will accept any host which will submit to its attack. Bishopp (1913) observed that cattle with low numbers of stable flies on them were more nervous than the average of the herd. He stated that the nervous individuals seemed to ward off fly attacks by their frequent movements.

Bax (1937) found that the tsetse fly, Glossina swynnertoni (Austen), a related species to the horn fly, was sensitive to the scent and sight of oxen even at great distances. He demonstrated that the tsetse fly contained in a grass cage reacted to oxen passing windward at distances up to 180 ft. The sight of oxen at distances up to 450 ft. also stimulated reactions in this tsetse fly. From the sight tests, Bax concluded that the criterion of distance at which a reaction was produced was the tonal contrast between the oxen and their background.

Instances of bovine resistance to ticks and arthropod-borne diseases are found in the literature. This gives additional support to the feasibility of fly susceptibility. Bonsma (1949) compared the susceptibility of Afrikander and exotic cattle to ticks by making monthly counts of 12 cows of each breed for 12 consecutive months. He found that the number of ticks on Afrikander cattle was remarkably lower than on exotic breeds.

Bonsma attributed this largely to the comparatively thick skin of the Afrikanders which was less attractive to ticks. West African Short-horns, partly of Zebu blood, were found to be much more resistant to trypanosomiasis than cattle from areas where the tsetse fly, the vector of trypanosomes, is not prevalent (Stesart, 1951).

In other studies of disease resistance, Lush (1950) has found the average intra-herd regression of daughter on dam within 27 dairy herds in New Zeland was 0.19 for mastitis resistance. By doubling the regression coefficient the estimate of heritability is 0.35. Legates and Grinnells (1952) studied data from 11 North Carolina herds involving 956 cows and obtained an estimate of the heritability of resistance to mastitis of 0.27 \hat{z} 0.10. White and Ibsen (1934), Murphy et al. (1944), and Reid (1954) have also concluded that inheritance is an important factor in the determination of resistance to mastitis in dairy cattle.

METHODS AND MATERIALS

SOURCE OF DATA

FLY COUNTS:

To utilize as many data as possible in making heritability estimates, fly counts collected from the lactating dairy herd at Oklahoma State University during previous years were used. Counts of the house fly, Musca domestica Linn., the stable fly, Stomoxys calcitrans (Linn.), and the horn fly, Siphona irritans (Linn.), which had been initially recorded for the purpose of testing fly repellents during the years of 1953, 1954, 1957, and 1958 were used in this study. It can be readily seen that fly counts taken under the influence of repellent action could not be used as a true measure of normal susceptibility. This made it necessary to abstract only those counts which were made either before repellents had been applied or after they were no longer effective. For the most part, only pre-treatment counts which had been made in order to balance groups of cows for fly susceptibility were used. During several years sufficient data of this kind were not available. In this case, time of repellent application served as the major criterion of count differentiation. No counts were used that had been collected less than 72 hours after the application of repellent. Other factors taken into consideration in selecting these data were the level of fly population present and the amount of data needed to determine normal fly susceptibility.

Fly counts were also recorded by the author during the 1959 fly season. The number of cows used in this study and times counted per year

for each breed are given in Tables I and II, respectively. It can be seen in Table I that the Guernsey and Jersey breeds were not counted in 1954, 1957, and 1958. Likewise, Ayrshires were not counted in 1957 and 1958.

TABLE I
THE NUMBER OF COWS COUNTED PER YEAR FOR EACH BREED
USED IN THIS STUDY

Breed	1953	1954	1957	1958	1959	All-years
Ayrshire	23	23	--	--	23	69
Guernsey	20	--	--	--	27	47
Holstein	30	32	34	26	41	163
Jersey	16	--	--	--	17	33
Total	89	55	34	26	108	312

--Fly counts not taken.

TABLE II
THE NUMBER OF FLY COUNTS PER YEAR USED TO DETERMINE NORMAL
FLY SUSCEPTIBILITY FOR COWS OF EACH BREED

Breed	1953	1954	1957	1958	1959
Ayrshire	15	19	--	--	32
Guernsey	14	--	--	--	30
Holstein	28	27	28	19	26
Jersey	15	--	--	--	31

--Fly counts not taken.

As previously stated, the number of fly counts per year for each breed is given in table II. The range was from 14 for Guernseys in 1953 to 32 for Ayrshires in 1959. It should be pointed out here that the difference in the number of counts did not influence the determination of normal fly susceptibility to a very large extent because average numbers of flies were used. The averages were obtained by dividing yearly totals by the number of counts made.

Counts of all three fly species were made simultaneously by visual observation of individual cows. The horn fly can be readily differentiated from the other two species because of its smaller size. The horn fly is about four mm long (Herms, 1950). The stable fly and house fly are somewhat more difficult to distinguish because of their similarity in color and size. However, certain characteristics may be used to separate these species under field conditions. As pointed out by Herms, the stable fly spreads its wing tips farther apart and has its head thrown well up when at rest. The stable fly, being a blood sucker, feeds primarily in one spot and thus, is less robust in its movements over the body surface of the cow than the house fly. The portion of the body of the cow on which the fly is found may also serve as an indicator of the species in question. The stable fly is rarely, if ever, found on the backs of cattle; whereas, the house fly may be found there in large numbers under certain conditions.

The numbers of each species found on the whole body area of the cow, excluding the head and udder, were recorded for an entire breed within a one-hour period. This would tend to eliminate large environmental variations due to fluctuating fly population levels. Head and udder areas were not counted because a portion of the data was initially

collected for the purpose of repellency testing. These areas were not considered because repellents were not applied to them. Fly count data recorded in 1959 were taken in a like manner to avoid inconsistency in counting technique.

RELATIONSHIP OF COWS:

Fly counts observations during the five-year period were recorded according to the neck chain numbers of individual cows. The identification of these cows was made by checking monthly milk sheets for each breed during the period mentioned above. From the milk sheets, the name and any changes in neck chain number were obtained. The cows were then identified in their respective breed herd books.

From the pedigrees of cows for which fly count data were available, paternal half-sib and dam-daughter relationships were obtained for use in making heritability estimates. The numbers of paternal half-sibs found and sires represented for each breed are given in table III. This table illustrates the limited number of records that was available for a study of this nature. Because of this, all four breeds were combined to give over-all estimates of heritability in addition to those estimates yielded for the various breeds.

The numbers of intra-sire, dam-daughter pairs and sires represented for each breed are given in table IV. Here again all breeds were combined to give over-all estimates of heritability, as well as, those estimates for each breed.

Lush (1948) states that an estimate of the environmental correlation may be had by computing the correlation between unrelated herd mates. Thus, in order to obtain as much accuracy as possible in making herita-

bility estimates, correlation studies were made on unrelated cows of the same breed. Approximately half of the intra-sire, dam-daughter pairs given in table IV were on an intra-year basis; therefore, the correlation study of unrelated pairs was designed to simulate this condition. The number of intra-year and inter-year unrelated pairs used to estimate correlation of environmental variance for the respective breeds is given in table V. From this table, it can be noted that the number of unrelated pairs for each breed compare favorably in proportion to the number of respective dam-daughter pairs found in table IV.

TABLE III

THE NUMBER OF PATERNAL HALF-SIBS AND SIREs USED TO ESTIMATE
HERITABILITY OF FLY SUSCEPTIBILITY FOR EACH BREED

Breed	Paternal Half-sibs	Sires
Ayrshire	52	5
Guernsey	30	5
Holstein	98	5
Jersey	25	8
Total	205	23

TABLE IV

THE NUMBER OF INTRA-SIRE, DAM-DAUGHTER PAIRS AND SIREs USED TO ESTIMATE HERITABILITY OF FLY SUSCEPTIBILITY FOR EACH BREED

Breed	Dam-daughter Pairs	Sires
Ayrshire	18	4
Guernsey	11	4
Holstein	29	6
Jersey	7	6
Total	65	20

TABLE V

THE NUMBER OF INTRA-YEAR AND INTER-YEAR UNRELATED PAIRS USED TO ESTIMATE CORRELATION OF ENVIRONMENTAL VARIANCE IN EACH BREED

Breed	Intra-year Pairs	Inter-year Pairs	Total Pairs
Ayrshire	15	10	25
Guernsey	6	12	18
Holstein	20	20	40
Jersey	5	7	12
Total	46	49	95

PHENOTYPIC CORRELATIONS:

To study the influence of certain physical characteristics of dairy cows on the various fly species, phenotypic correlations were made. Factors studied were skin thickness, white-spotting and age. Obviously white-spotting was studied in the Ayrshire and Holstein breeds, only. The fly counts used in this study were taken in 1959 and are given in table II. The number of cows for each breed used in making phenotypic correlations was as follows:

<u>Breed</u>	<u>Number</u>
Ayrshire	18
Guernsey	19
Holstein	34
Jersey	12
<hr/>	
Total	83

The skin thickness of individual cows was determined by taking a total of seven measurements on each cow. The technique employed consisted of measuring a fold of skin with the aid of a micrometer equipped with a ratchet. The ratchet was used to obtain consistency in the amount of exerted pressure on the skin. Added precision was given by rotating the ratchet at approximately the same speed and reading the micrometer immediately following the initial click during each measurement. Micrometer readings were made by one person and recordings by another in order to avoid biased readings.

The total of seven measurements of skin thickness were obtained as follows: one from each side of the neck approximately six inches anterior to the point of the shoulder; one from each side over the last rib in the region of the side; and three from the skin of the escutcheon at a point approximately seven inches below the anal region.

It was noted that all of the cows in this particular investigation had shed their winter hair coats at the time that the skin thickness determinations were made; therefore, the readings were not influenced by large differences in length of haircoat. All measurements for the different areas, i.e., neck, side, and escutcheon, were taken on all breeds within a three-hour period of the same day. This would tend to eliminate possible fluctuations in skin thickness due to ambient temperatures or other environmental conditions.

Briquet and Lush (1947) found that visual estimates of white-spotting in Holstein-Friesian cattle at different ages gave a repeatability¹ of 0.982. With this in mind, visual estimates were made by two judges which were combined to give an average percentage of white-spotting.

Ages of all cows at the time fly counts were made were recorded to the nearest month from calving dates found in the respective breed herdbooks.

Statistical Procedures

One of the major problems in most studies of inheritance is to control environmental conditions so that phenotypic measurements may be used as reliable estimates of genotype. Because of the physical impossibilities of controlling environmental conditions in studies of this nature, it behooves the investigator to use those statistical analyses best suited to eliminate differences in environment. The analysis of variance, yearly correction for fly population levels, and correlation of unrelated herd mates were used in this study in an

¹Repeatability used here refers to the correlation between different visual estimates of individual cows at various ages.

attempt to eliminate environmental differences. These procedures will be discussed under the appropriate methods of estimating heritability for which they were employed.

Lush (1940) states that the idea of heritability takes into consideration whether the differences actually observed between individuals are due to different genotypes or exposure to different environmental forces. Lush also defines heritability in both a broad and narrow sense. In the broad sense, heritability refers to the functioning of the genotype as a whole and includes that portion of the total variance due to dominance, epistasis and non-linear combination effects (interactions) of genotypic and environmental differences. The definition of heritability in the narrow sense is the ratio of only the additive genetic variance to the total phenotypic variance. Figure 1 from Lush (1940) illustrates more clearly the difference between the two definitions; however, it should be pointed out that the relative proportions of the observed variance chosen by Lush are arbitrary.

According to Lush (1948), an actual numerical estimate of heritability is usually somewhere between the narrow and the broad definitions. It almost always includes a little of the epistatic variance and sometimes a small portion of the dominance variance. The numerical estimate may include all, part, or none of the variance caused by the non-linear effects of heredity and environment. The proportions of the non-additive variance included in the numerical estimate will depend on the method used to estimate heritability.

Fractions of the Observed Variance

σ_G^2	σ_D^2	σ_I^2	σ_{EH}^2	σ_E^2
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σ_G^2	σ_D^2	σ_I^2	σ_{EH}^2	σ_E^2
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Heritability in the Broad Sense

σ_G^2

σ_G^2	σ_D^2	σ_I^2	σ_{EH}^2	σ_E^2
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Heritability in the Narrow Sense

FIGURE 1. Meanings of Heritability in the Broad and Narrow Sense Where:

- σ_G^2 = additively genetic variance
- σ_D^2 = variance due to dominance deviations
- σ_I^2 = variance due to epistatic interactions
- σ_{EH}^2 = variance due to non-linear interactions of heredity and environment
- σ_E^2 = variance due to environmental variations.

PATERNAL HALF-SIB CORRELATIONS:

Correlation between relatives was first used by Galton and has never fallen entirely into disuse, although investigators now have a better understanding of the need of discounting environmental correlations and for correctly appraising mating systems. Lush (1948) states that heritability may be estimated from the half-sib correlation by multiplying by four. This is done because the genic value of half-sibs is expected to

be only one-fourth. Unfortunately, as mentioned by Lush, the multiplication by four magnifies any error due to sampling or environmental correlation.

The statistical method used to estimate paternal half-sib correlation was that of computing intraclass correlation, as described by Snedecor (1946), from the analysis of variance.

Two different paternal half-sib studies were made. One consisted of analyzing each breed separately on an intra-year, intra-sire basis. The other study included all four breeds and the analysis was made on an intra-year, intra-breed, intra-sire basis. Lush (1948) states that if data are collected from several herds or over a period of several years the assumption can often be made that the intra-herd, intra-year analysis has done away with environmental correlations between paternal half-sibs. In these data the collection was from a single herd.

The information that was used in the paternal half-sib method of estimating heritability and how it was punched on International Business Machine cards was as follows:

<u>Column Number</u>	<u>Information Recorded</u>
1-4	Project number
5-8	Year of fly count
9-12	Breed number
13-16	Sire number
17-20	Daughter number
31-35	Total number of house flies
36-40	Total number of stable flies
41-45	Total number of horn flies
46-50	Number of fly counts
66-70	Average number of house flies*
71-75	Average number of stable flies*
76-80	Average number of horn flies*

*Variables used in making heritability estimates.

The model for the Analysis of Variance (Intra-year, Intra-sire)

was as follows:

Source	d.f.	Expected Mean Square
Total	$N - 1$	
Years	$y - 1$	$\sigma_e^2 + k_2 \sigma_s^2 + k_3 \sigma_y^2$
Sires in years	$\sum_i s_i - y$	$\sigma_e^2 + k_1 \sigma_s^2$
Daughter in sires	$\sum_i \sum_j n_{ij} - \sum_i s_i$	σ_e^2

where:

$$\hat{\sigma}_s^2 = \frac{\text{M.S. between sires} - \text{M.S. daughters}}{k_1}$$

$$\text{and: } k_1 = \frac{\sum_i \sum_j n_{ij}^2 \left[\frac{1}{n_{ij}} - \frac{1}{n_i} \right]}{\sum_i s_i - y}$$

$$k_2 = \frac{\sum_i \sum_j n_{ij}^2 \left[\frac{1}{n_i} - \frac{1}{N} \right]}{y - 1}$$

$$k_3 = \frac{\sum_i n_i^2 \left[\frac{1}{n_i} - \frac{1}{N} \right]}{y - 1}$$

 y = number of years s_i = number of sires in i^{th} year n_{ij} = number of daughters for the j^{th} sire in the i^{th} year N = total number of daughters.The intraclass correlation coefficient $(r) = \frac{\hat{\sigma}_s^2}{\hat{\sigma}_s^2 + \hat{\sigma}_e^2}$ $4(r)$ = heritability.

The model for the Analysis of Variance (Intra-year, Intra-breed,

Intra-sire) was as follows:

Source	d.f.	Expected Mean Square
Total	$N - 1$	
Years	$y - 1$	$\sigma_e^2 + k_4 \quad \sigma_s^2 + k_5 \quad \sigma_b^2 + k_6 \sigma_y^2$
Breeds in years	$\sum_i b_i - y$	$\sigma_e^2 + k_2 \quad \sigma_s^2 + k_3 \quad \sigma_b^2$
Sires in breeds	$\sum_i \sum_j s_{ij} - \sum_i b_i$	$\sigma_e^2 + k_1 \quad s^2$
Daughters in sires	$\sum_i \sum_j \sum_k n_{ijk} - \sum_i \sum_j s_{ij}$	σ_e^2

where:

$$\hat{\sigma}_s^2 = \frac{\text{M.S. between sires} - \text{M.S. daughters}}{k_1}$$

$$\text{and: } k_1 = \frac{\sum_i \sum_j \sum_k n_{ijk}^2 \left[\frac{1}{n_{ijk}} - \frac{1}{n_{ij}} \right]}{\sum_i \sum_j s_{ij} - \sum_i b_i}$$

$$k_2 = \frac{\sum_i \sum_j \sum_k n_{ijk}^2 \left[\frac{1}{n_{ij}} - \frac{1}{n_i} \right]}{\sum_i b_i - y}$$

$$k_3 = \frac{\sum_i \sum_j n_{ij}^2 \left[\frac{1}{n_{ij}} - \frac{1}{n_i} \right]}{\sum_i b_i - y}$$

$$k_4 = \frac{\sum_i \sum_j \sum_k n_{ijk}^2 \left[\frac{1}{n_i} - \frac{1}{N} \right]}{y - 1}$$

$$k_5 = \frac{\sum_i \sum_j n_{ij}^2 \left[\frac{1}{n_i} - \frac{1}{N} \right]}{y - 1}$$

$$\sum_i \frac{n_i^2}{n_i} \left[\frac{1}{n_i} - \frac{1}{N} \right]$$

$$k_6 = \frac{\quad}{y - 1}$$

The models for the analysis of variance on the preceding pages were obtained from Pulley (1959).

y = number of years

b_i = number of breeds in the i^{th} year

s_{ij} = number of sires in the j^{th} breed in the i^{th} year

n_{ijk} = number of daughters in the k^{th} sire in the j^{th} breed in the i^{th} year

n_{ij} = number of daughters in the j^{th} breed in the i^{th} year

n_i = number of daughters in the i^{th} year

N = total number of daughters.

The intraclass correlation coefficient (r) =
$$\frac{\hat{\sigma}_s^2}{\hat{\sigma}_s^2 + \hat{\sigma}_e^2}$$

$4(r)$ = heritability.

INTRA-SIRE CORRELATIONS OF DAUGHTER WITH DAM:

This method of estimating heritability was first introduced by Lush (1940). The estimate of heritability is made by doubling the correlation coefficient. As stated by Lush, this is essentially a parent-offspring resemblance but computing it on an intra-sire basis goes far toward automatically discounting environmental contributions and any peculiarities of the mating system. Such difficulties are avoided by restricting the analysis to such variance as is found within groups of females which get mated to one sire. No attempt is made to analyze the hereditary or environmental mean differences which exist between such groups of females.

Other advantages of the intra-sire correlation of daughter with dam method of estimating heritability mentioned by Lush are: (1) the resemblance between parents and offspring does not include dominant deviations and (2) that sampling errors are less serious because the correlation coefficient is multiplied by two instead of four as in the paternal half-sib method.

In this phase of the heritability studies it was found that the number of dam-daughter pairs counted within the same years were too limited to make an appropriate analysis on an intra-year basis. Thus, both intra-year and inter-year dam-daughter pairs were combined in estimating heritability. The difficulty that arose in this case was in avoiding environmental correlations due to yearly differences in fly population levels. Since it is customary to correct data of this nature for known environmental effects, it would seem valid to apply correction factors to the data in this study wherein reasonably accurate estimates could be made of environmental differences.

The procedure used was that of computing yearly corrections factors from yearly herd averages and adjusting all data to a pre-selected base year. The number of cows per year of each breed used in computing correction factors can be found in table I under the appropriate section of Source of Data. The yearly correction factors for each fly species used to adjust data for intra-sire, dam-daughter pairs are given in tables VI, VII, and VIII.

After yearly corrections were made, two different types of analysis were used in estimating heritability. One was the intra-sire analysis for each breed and the other was an intra-breed, intra-sire analysis using all four breeds as one group to obtain over-all estimates of heritability.

TABLE VI

YEARLY CORRECTION FACTORS FOR HOUSE FLY POPULATION LEVELS OF
INTRA-SIRE, DAM-DAUGHTER PAIRS IN EACH BREED

Breed	1953	1954	1957	1958	1959
Ayrshire	1.00	5.18	--	--	147.11
Guernsey	1.00	--	--	--	32.81
Holstein	1.00	5.51	138.09	5.70	52.66
Jersey	1.00	--	--	--	183.13

--Fly counts not taken.

TABLE VII

YEARLY CORRECTION FACTORS FOR STABLE FLY POPULATION LEVELS OF
INTRA-SIRE, DAM-DAUGHTER PAIRS IN EACH BREED

Breed	1953	1954	1957	1958	1959
Ayrshire	1.00	.29	--	--	.85
Guernsey	1.00	--	--	--	.55
Holstein	1.00	.77	4.15	3.32	1.82
Jersey	1.00	--	--	--	.67

--Fly counts not taken.

TABLE VIII

YEARLY CORRECTION FACTORS FOR HORN FLY POPULATION LEVELS OF
INTRA-SIRE, DAM-DAUGHTER PAIRS IN EACH BREED

Breed	1953	1954	1957	1958	1959
Ayrshire	1.00	.33	--	--	.79
Guernsey	1.00	--	--	--	1.10
Holstein	1.00	.35	1.44	.73	1.68
Jersey	1.00	--	--	--	.48

--Fly counts not taken.

As was mentioned earlier, Lush (1948) points out that estimates of the environmental variance may be had by computing correlation between unrelated herd mates. To further remove yearly differences in fly population levels and any other environmental differences, correlations of this nature were made. The yearly correction factors were applied to unrelated pairs in the same manner as with dam-daughter pairs. The two types of analysis previously described for intra-sire, dam-daughter pairs were employed for computing correlation on unrelated herd mates. The number of intra-year and inter-year unrelated pairs used to estimate correlation of environmental variance in each breed can be seen in table V in the proper section of Source of Data. The appropriate estimates of environmental variance were then subtracted from correlations yielded by intra-sire, dam-daughter pairs before multiplying by two to estimate heritability.

$$\text{Heritability} = 2 (r_1 - r_2)$$

where:

r_1 = correlation coefficient of dam-daughter pairs

r_2 = correlation coefficient of unrelated pairs.

PHENOTYPIC CORRELATIONS:

Two types of analysis were made in the phenotypic correlation study. One consisted of computing correlation within each breed. The other analysis considered all breeds as one group.

The information that was used in these analyses and how it was punched on International Business Machine cards was as follows:

<u>Column Number</u>	<u>Information Recorded</u>
1-4	Project number
5-6	Breed number of cow
7-10	Cow number
11-13	Escutcheon skin thickness
14-16	Side skin thickness
17-19	Neck skin thickness
20-23	Over-all skin thickness
24-27	White-spotting*
28-32	Average number of house flies
33-37	Average number of stable flies
38-42	Average number of horn flies
43-46	Total number of house flies
47-50	Total number of stable flies
51-54	Total number of horn flies
55-56	Number of fly counts
57-59	Age of cow in months
72-80	Computing center number

*Recorded in the Ayrshire and Holstein breeds, only.

DISCUSSION OF RESULTS

PATERNAL HALF-SIB ESTIMATES:

Estimates of heritability of susceptibility to the various fly species for each breed can be obtained by multiplying the respective intraclass correlation coefficients given in table IX by four. The correlations of paternal half-sibs were derived from the analyses of variance given in appendix A. Correlation was calculated as the ratio of the variance between sires to the total variance.

$$\text{The intraclass correlation coefficient (r)} = \frac{\hat{\sigma}_s^2}{\hat{\sigma}_s^2 + \hat{\sigma}_e^2}$$

TABLE IX

PATERNAL HALF-SIB CORRELATIONS OF FLY SUSCEPTIBILITY
FOR EACH BREED

Breed	House Fly	Stable Fly	Horn Fly
Ayrshire	-.184	.021	-.150
Guernsey	-.128	.021	.199
Holstein	-.069	-.025	.050
Jersey	-.403	.093	.448
All-breeds*	-.170	-.026	-.065

*Above breeds combined to form one group.

From table IX it can be seen that all correlations of house fly susceptibility were negative. These ranged from $-.069$ in Holsteins to $-.403$ in Jerseys. These correlations multiplied by four would obviously be underestimates of heritability. Lush (1948) states that the paternal half-sib correlation is merely a way of expressing how much smaller the variance is between paternal half-sibs than between non-sibs. In these estimates the mean square values (between sires) were smaller than the respective variance components for paternal half-sibs. This would suggest that the analyses of variance were not efficient in removing all of the environmental variance. This assumption would seem more logical since fly population levels in this species were more variable than in the other species considered.

Correlations of stable fly susceptibility from table IX seem to yield somewhat more realistic estimates of heritability than those for the house fly. The correlations ranged from $-.025$ for Holsteins to $.093$ for Jerseys. The negative correlation of $-.025$ obtained for Holsteins multiplied by four would give $-.10$ heritability. This would suggest that there was no resemblance between stable fly susceptibility and genotype for the cows used in this study. Identical correlations of $.021$ were obtained for the Ayrshire and Guernsey breeds. These yield estimates of heritability of $.084$ which indicate that very limited progress would be expected in selecting for this trait on the basis of fly counts. The highest correlation of phenotypic and genotypic differences for stable fly susceptibility was found in Jerseys. Here the multiplication by four gave $.37$ heritability. However, it should be mentioned that the limited amount of data available for this breed did not render the mean square value (between sires) statistically signifi-

cant at the 5% level. When all breeds were pooled the correlation of stable fly susceptibility was $-.026$. The negative correlation obtained for Holsteins which comprised approximately half of the data, as well as, the addition of breed differences in environment to the analysis of variance would help explain a negative value in this case.

The largest range in paternal half-sib correlations occurred in horn fly susceptibility. These varied from $-.150$ in Ayrshires to $.448$ in Jerseys. The highly negative correlation obtained for Ayrshires would again point to the probably inefficiency of the analysis of variance in discounting all of the variance due to the environmental term. A heritability estimate of $.20$ was obtained for horn fly susceptibility; thus indicating a portion of the differences between parents could be expected to be recovered in their offspring. Correlation coefficients of $.199$ and $.448$ were obtained for the Guernsey and Jersey breeds, respectively. These, multiplied by four, would give $.80$ heritability for Guernseys and 1.79 for Jerseys. Since an estimate of heritability cannot theoretically exceed one it becomes obvious that the value of 1.79 is a gross overestimate in this case. A partial explanation of the high estimates of heritability obtained for these breeds may be had by examining the breakdown of daughters within sires for the various years given in appendix B. In the Guernsey breed it can be seen that only sire number 2 had daughters counted in both 1953 and 1959. Daughters of sire 1 were subjected to different environments than those of sires 3, 4, and 5. This situation is also somewhat more true in Jerseys than in Ayrshires and Holsteins. This would have a tendency to raise heritability by increasing the variance component between non-sibs and/or decreasing the component for half-sibs.

Another reason for discrepancy in heritability estimates according to Lush (1940) is the sampling error. This factor becomes of a more serious nature when limited amounts of data are used, as in the case of this study. Also, as previously mentioned in the Methods and Materials, this cause of discrepancy even becomes more serious in the paternal half-sib method because of the multiplication by four.

The all-breed estimate of heritability of horn fly susceptibility was -.26. This, along with the negative all-breed estimates for house fly and stable fly susceptibility, suggest that it would not be feasible to select for fly susceptibility in dairy cattle on the basis of normal susceptibility determined by fly counts.

INTRA-SIRE CORRELATION ESTIMATES:

Estimates of heritability of susceptibility to the various fly species for each breed can be found by subtracting correlations of unrelated herd mates (table X) from their respective intra-sire, dam-daughter correlations (table XI) and multiplying the difference by two. The variances and covariances used to compute correlation for unrelated and dam-daughter pairs are given in appendix C.

$$\text{Heritability} = 2 (r_1 - r_2)$$

where:

r_1 = correlation coefficient of dam-daughter pairs

r_2 = correlation coefficient of unrelated pairs.

Table X shows that correlations for unrelated pairs are inconsistent. In some cases this would point to the inefficiency of the yearly correction factors in eliminating environmental differences. Also, sampling error may be prevalent in some of these estimates of environmental

TABLE X
UNRELATED PAIR CORRELATIONS OF FLY SUSCEPTIBILITY
FOR EACH BREED

Breed	House Fly	Stable Fly	Horn Fly
Ayrshire	.114	-.092	.016
Guernsey	.185	.143	.035
Holstein	-.076	-.054	.312
Jersey	-.641	-.314	.037
All-breeds*	.185	.538	.441

*Above breeds combined to form one group.

TABLE XI
INTRA-SIRE, DAM-DAUGHTER CORRELATIONS OF FLY
SUSCEPTIBILITY FOR EACH BREED

Breed	House Fly	Stable Fly	Horn Fly
Ayrshire	.392	.250	.238
Guernsey	.162	-.256	.310
Holstein	-.019	-.066	.139
Jersey	-.443	.500	.527
All-breeds*	.192	.459	.319

*Above breeds combined to form one group.

variance. When all breeds were considered as one group, the correlations of fly susceptibility were somewhat larger because of the correlation of environmental peculiarities within breeds. This was true for both unrelated and dam-daughter pairs.

Estimates of heritability of house fly susceptibility ranged from $-.05$ in Guernseys to $.56$ in the Ayrshire breed. The comparison of correlations for unrelated and dam-daughter pairs in Guernseys indicate that all of the resemblance between phenotypes was due only to environmental effect. Correlations for the other breeds were larger for related than unrelated pairs. Heritability estimates of house fly susceptibility for Holsteins and Jerseys were $.11$ and $.40$, respectively. These plus the estimate found for Ayrshires suggest that a portion of the resemblance between dams and daughters was genetic in origin; thus, indicating the feasibility of selection. However, the all-breed estimate of heritability was $.01$. The sampling error is probably of a less serious nature in this estimate because of the increased amount of data.

In contrast to the paternal half-sib study, the heritability estimates of stable fly susceptibility were more variable than with the other fly species. The extremes in this case were from $-.80$ in Guernseys to 1.63 in Jerseys. The estimate of $-.80$ was due mostly to the negative correlation of dam-daughter pairs of $-.256$ (table XI). This estimate was even made more highly negative because of the subtraction of the respective correlation of $.143$ found for unrelated pairs (table X). Heritability cannot theoretically be less than zero; thus, the estimate of $-.80$ would be considered a gross underestimate and is probably due to sampling error. Likewise, as pointed out in the paternal half-sib method, heritability cannot exceed one and, therefore the estimate of

1.63 is a gross overestimate for stable fly susceptibility in Jerseys. A large portion of the overestimate can be attributed to the correlation of unrelated pairs which was $-.314$ (table X). A high estimate of $.68$ was also obtained for Ayrshires. However, negative heritability estimates of stable fly susceptibility of $-.02$ and $-.16$ were yielded for Holsteins and all-breeds, respectively.

Table XI shows that dam-daughter correlations for horn fly susceptibility were positive. However, larger correlations were found for unrelated pairs in the case of Holsteins and all-breeds (table X). This gave negative estimates of $-.35$ and $-.24$ for these breeds, respectively. This infers that all of the resemblance between dam-daughter pairs was due only to environmental effect. Contrasting heritability estimates of $.44$, $.55$, and $.98$ were obtained for Ayrshires, Guernseys, and Jerseys, respectively. These indicate the feasibility of selection for horn fly susceptibility on a fly count basis.

A resemblance was noted between the all-breed heritability estimates yielded by the two methods of estimating heritability. The estimates for the paternal half-sib method were $-.68$, $-.10$, and $-.26$ for house fly, stable fly, and horn fly susceptibility, respectively. Those from the intra-sire, dam-daughter correlation method were $.01$, $-.16$, and $-.24$ for house fly, stable fly, and horn fly susceptibility, respectively. These over-all estimates indicate that little or no progress could be expected from a selection program for these traits.

PHENOTYPIC CORRELATIONS:

The influence of skin thickness, white-spotting, and age on individual cow susceptibility to the various species of flies was studied through the use of phenotypic correlations. The values of the

above factors obtained within each breed are found in appendix D. The corrected sums of squares and cross products used to compute correlation between the various factors can be seen in appendix E.

The correlations of the various physical characteristics of the dairy cow with house fly susceptibility are given in table XII. The correlation of age with house fly susceptibility yielded positive results in every breed except Guernseys. The highest correlation was obtained for Jerseys, but the smaller number included in this breed did not render the correlation coefficient statistically significant. A correlation of .218 was significant for the all-breed group which indicates that the older cows were slightly more susceptible to house fly attack than younger cows in this case.

TABLE XII

CORRELATIONS OF AGE, WHITE-SPOTTING AND SKIN THICKNESS WITH HOUSE FLY SUSCEPTIBILITY FOR EACH BREED

Breed	Age	White-Spotting	Skin Thickness
Ayrshire	.053	-.596**	-.273
Guernsey	-.259	---	-.321
Holstein	.296	-.296	.010
Jersey	.386	---	-.493
All-breeds ¹	.218*	-.331**	-.087

¹Above breeds combined to form one group.

---No measurement.

* Significant at the 5% level.

**Significant at the 1% level.

From table XII, it can be seen that a highly significant negative correlation of $-.596$ was found between white-spotting and house fly susceptibility in the Ayrshire breed. Snedecor (1946) states that negative values of the correlation coefficient indicate that large values of one variable are associated with small values of another variable. The interpretation here suggests that low values of white-spotting are closely associated with high house fly susceptibility. The correlation estimate of $-.296$ was not significant in the Holstein breed with respect to this factor. The all-breed estimate which included Ayrshires and Holsteins, only, was a highly significant value of $-.331$. This value is in line with the color preference tests made by Freeborn and Berry (1935), and Harsham (1946) who found that the house fly prefers dark to light colors when identical physical surfaces are involved.

As was expected, since the house fly does not pierce the skin, no significant correlations were obtained between skin thickness and house fly susceptibility. However, the correlations of $-.273$, $-.321$, and $-.493$ for the Ayrshire, Guernsey, and Jersey breeds, respectively, cannot be overlooked. These could be due to an association between the house fly and the other species under consideration. Data of this nature will be presented in the next section of the Discussion of Results.

It is suggested that the investigator consider white-spotting in Holsteins and Ayrshires when balancing groups of cows for testing chemicals against house flies. Age should be considered to a lesser degree in this regard when any of all of these breeds are used for testing purposes. The all-breed estimate of $-.087$ indicates that skin thickness

need not be considered.

The correlations of the various factors with stable fly susceptibility are given in table XIII. All correlations of age with stable fly susceptibility were positive except in Guernseys. The highest correlation was that of .505 for Holsteins. The all-breed correlation was .395 as compared to the value of .238 when house fly susceptibility was considered.

TABLE XIII

CORRELATIONS OF AGE, WHITE-SPOTTING AND SKIN THICKNESS WITH STABLE FLY SUSCEPTIBILITY FOR EACH BREED

Breed	Age	White-Spotting	Skin Thickness
Ayrshire	.393	-.787**	-.216
Guernsey	-.030	---	-.340
Holstein	.505**	-.669**	-.070
Jersey	.399	---	-.420
All-breeds ¹	.395**	-.719**	-.285**

¹Above breeds combined to form one group.

**Significant at the 1% level.

---No measurement.

This table shows that highly significant correlations were found between white-spotting and stable fly susceptibility. The values of -.787, -.669, and -.719 for Ayrshires, Holsteins, and all-breeds, respectively, very definitely indicate that the stable fly preferred the darker colored cows.

The range of correlations of skin thickness with stable fly susceptibility was from $-.070$ in Holsteins to $-.420$ in Jerseys (table XIII). The negative correlations infer that large values of skin thickness are associated with low susceptibility to stable flies. A highly significant value of $-.285$ was obtained in the all-breed estimate.

The all-breed estimates of correlation suggest the consideration of all of these characteristics of dairy cattle when using these animals for testing purposes.

Table XIV gives the correlations of the various factors with susceptibility to the horn fly. This table shows that these correlations were very similar to those obtained for correlation of stable fly susceptibility (table XIII). Therefore, these factors should be considered in balancing groups of cows for the testing of chemicals.

TABLE XIV

CORRELATION OF AGE, WHITE-SPOTTING AND SKIN THICKNESS WITH
HORN FLY SUSCEPTIBILITY FOR EACH BREED

Breed	Age	White-Spotting	Skin Thickness
Ayrshire	.301	$-.352$	$-.216$
Guernsey	$-.104$	---	$-.460$
Holstein	.313	$-.744^{**}$	$-.056$
Jersey	.220	---	$-.806$
All-breeds ¹	$.238^*$	$-.543^{**}$	$-.288^{**}$

¹Above breeds combined to form one group.

---No measurement.

*Significant at the 5% level.

**Significant at the 1% level.

The importance of determining normal fly susceptibility for dairy cattle to be used in the testing of fly sprays was pointed out by Pearson et al. (1933). They suggest the use of fly counts. The correlations obtained in this study indicate that age, white-spotting, and skin thickness should also be considered in attempting to balance such groups of cows for fly susceptibility.

CORRELATION OF FLY SPECIES ON COWS:

The preceding section suggests that the species of flies under consideration are somewhat attracted and/or repelled by the same physical factors. Therefore, correlations of the average number of different species of flies found on individual cows were studied. These would indicate the amount of efficiency to be expected in balancing groups of cows for more than one species. These correlations are presented in table XV. The corrected sums of squares and cross products used in computing these correlations are given in appendix E.

TABLE XV

CORRELATIONS BETWEEN AVERAGE HOUSE FLY, STABLE FLY AND HORN FLY NUMBER ON INDIVIDUAL COWS OF EACH BREED

Breed	House Fly- Stable Fly	House Fly- Horn Fly	Horn Fly- Stable Fly
Ayrshire	.742**	.322	.571*
Guernsey	.709**	.589*	.304
Holstein	.349*	.399*	.795**
Jersey	.304	.494	.298
All-breeds ¹	.422**	.158	.558**

¹Above breeds combined to form one group.

*Significant at the 5% level.

**Significant at the 1% level.

Table XV on the preceding page shows that correlations between average house fly and stable fly numbers were highly significant in the Ayrshire and Guernsey breeds. This tends to help explain the correlations of house fly susceptibility with skin thickness within these breeds (table XII). The correlation of the above species yielded more medium values of .349 and .304 in the Holstein and Jersey breeds, respectively. The all-breed value of .422 was highly significant. This suggests the feasibility of selecting cows for both house fly and stable fly susceptibility. The correlations of these two species are in line with the observations of Mayne (1913) and West (1951) who reported house flies feeding on blood droplets in close association with stable flies. This does not necessarily mean that this is the primary factor responsible for the correlation in this study.

Correlations were smaller between the house fly and horn fly than with the former and stable flies for Ayrshires and Guernseys. The most noticeable difference in the correlation of these species was in the all-breed estimate. A much smaller value of .158 was obtained in this case. This suggests the difficulty of selecting cows for both house fly and horn fly susceptibility. Much larger correlations were obtained in the individual breed estimates, however.

Correlations between stable flies and horn flies were highly significant in Holsteins and all-breeds. These were .795 and .558, respectively. A significant correlation of .571 was found in Ayrshires. Somewhat smaller values of .304 and .298 were obtained in Guernseys and Jerseys, respectively. In general, these correlations infer that it would be feasible to select cows for both stable fly and horn fly susceptibility.

CORRELATIONS OF SKIN THICKNESS MEASUREMENTS:

Correlations of the various skin thickness measurements with total skin thickness were made to determine which measurement gave the best estimate of over-all skin thickness. These correlations are presented in table XVI. The corrected sums of squares and cross products used to compute correlation are given in appendix E.

TABLE XVI

CORRELATIONS OF ESCUTCHEON, SIDE, AND NECK MEASUREMENTS WITH TOTAL SKIN THICKNESS OF INDIVIDUAL COWS OF EACH BREED

Breed	Escutcheon	Side	Neck
Ayrshire	.795**	.785**	.836**
Guernsey	.653**	.813**	.667**
Holstein	.596**	.841**	.487**
Jersey	.613*	.874**	.758**
All-breeds ¹	.741**	.863**	.642**

¹Above breeds combined to form one group.

*Significant at the 5% level.

**Significant at the 1% level.

This table shows that all of the correlations of skin thickness measurements with their total were all highly significant except the escutcheon measurement in Jerseys which was significant at the 5% level. Snedecor (1946) states that is correlation due to common causes. Therefore, it would be expected to be somewhat high in many cases.

The highest correlation was found for the side measurement in every breed except Ayrshires. The all-breed correlations for escutcheon, side, and neck were .741, .863, and .642, respectively. These indicate

that the side measurement gave the best indication of over-all skin thickness.

SUMMARY AND CONCLUSIONS

Estimates of heritability and correlation of fly susceptibility with age, white-spotting, and skin thickness of dairy cattle were made in this study. Fly counts collected during 1953, 1954, 1957, 1958, and 1959 were utilized in determining normal fly susceptibility of individual cows. The paternal half-sib and intra-sire, dam-daughter correlation methods of estimating heritability were used. The breeds of dairy cattle used were Ayrshire, Guernsey, Holstein, and Jersey. Data for 205 paternal half-sibs and 65 dam-daughter pairs were pooled to give over-all, all-breed estimates of heritability, as well as those for individual breeds. The fly species under consideration were the house fly, Musca domestica Linn., the stable fly, Stomoxys calcitrans (Linn.), and the horn fly, Siphona irritans (Linn.).

Heritability estimates of fly susceptibility determined by the paternal half-sib method were as follows:

<u>Breed</u>	<u>House Fly</u>	<u>Stable Fly</u>	<u>Horn Fly</u>
Ayrshire	-.74	.08	-.60
Guernsey	-.51	.08	.80
Holstein	-.28	-.10	.20
Jersey	-1.61	-.10	1.79
All-breeds	-.68	-.10	-.26

Heritability estimates of house fly susceptibility are all obviously underestimates since heritability cannot theoretically be less than zero. The large discrepancy in these estimates was primarily attributed to the inefficiency of the analysis of variance in eliminating environmental differences between years.

The only estimate of stable fly susceptibility that indicates the feasibility of selection was .37 for Jerseys. Estimates for the other breeds approached zero in their value.

Heritability estimates of horn fly susceptibility ranged from -.60 in Ayrshires to 1.79 in Jerseys. These extremes are obviously unrealistic. Estimates of .80 and .20 in Guernseys and Holsteins, respectively, infer that horn fly susceptibility is heritable in these breeds.

The all-breed heritability estimates yielded by the paternal half-sib method suggest that little or no progress could be expected in selecting for fly susceptibility on a fly count basis.

Heritability estimates of fly susceptibility obtained from the intra-sire, dam-daughter method were as follows:

<u>Breed</u>	<u>House Fly</u>	<u>Stable Fly</u>	<u>Horn Fly</u>
Ayrshire	.56	.68	.44
Guernsey	-.05	-.80	.55
Holstein	.11	-.02	-.35
Jersey	.40	1.63	.98
All-breed	.01	-.16	-.24

Heritability estimates yielded by the intra-sire, dam-daughter correlation were somewhat consistently larger in the Ayrshire and Jersey breed estimates than those obtained by the paternal half-sib method. These estimates indicate the feasibility of selecting for lowered fly susceptibility in these breeds. In general, heritability estimates for Guernseys and Holsteins yielded by dam-daughter correlation were negative in value.

A resemblance was noted in the all-breed estimates obtained from both methods of estimating heritability. These estimates suggest that

it would not be feasible to decrease the fly susceptibility of dairy cattle by selection.

Positive correlations of age with fly susceptibility were obtained for all breeds except Guernseys. In general, highly negative correlations were found between white-spotting and fly susceptibility is closely associated with large values of white-spotting. Negative correlations were also obtained between stable fly and horn fly susceptibility with skin thickness values which indicate that thick skinned cows were less susceptible than thin skinned ones.

It is suggested that the above factors be taken into consideration when selecting dairy cows to be used in the testing of repellents or insecticides.

High values were yielded for house fly-stable fly and stable fly-horn fly correlations. These infer that some efficiency could be expected in selecting cows for testing purposes for susceptibility to more than one species.

Correlations of the various measurements of skin thickness i.e., escutcheon, side, and neck, with over-all skin thickness suggest that the side measurement was the best indication of over-all skin thickness.

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APPENDICES

APPENDIX A

TABLE XVII

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF HOUSE FLY
SUSCEPTIBILITY IN AYRSHIRES

Source	d.f.	M.S.	Expected (M.S.)
Total	53		
Years	2	2,100.409	
Sires in years	8	.793	$\sigma_e^2 + 4.517 \sigma_s^2$
Daughters in sires	43	2.652	σ_e^2

TABLE XVIII

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF HOUSE FLY
SUSCEPTIBILITY IN GUERNSEYS

Source	d.f.	M.S.	Expected (M.S.)
Total	29		
Years	1	2,277.164	
Sires in years	4	.486	$\sigma_e^2 + 3.916 \sigma_s^2$
Daughters in sires	24	.874	σ_e^2

TABLE XIX

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF HOUSE FLY
SUSCEPTIBILITY IN HOLSTEINS

Source	d.f.	M.S.	Expected (M.S.)
Total	95		
Years	4	1,638.268	
Sires in years	9	10.037	$\sigma_e^2 + 6.395 \sigma_s^2$
Daughters in sires	82	17.089	σ_e^2

TABLE XX

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF HOUSE FLY
SUSCEPTIBILITY IN JERSEYS

Source	d.f.	M.S.	Expected (M.S.)
Total	24		
Years	1	2,817.256	
Sires in years	9	1.214	$\sigma_e^2 + 2.145 \sigma_s^2$
Daughters in sires	14	3.167	σ_e^2

TABLE XXI

INTRA-YEAR, INTRA-BREED, INTRA-SIRE ANALYSIS OF VARIANCE OF
HOUSE FLY SUSCEPTIBILITY IN ALL-BREEDS*

Source	d.f.	M.S.	Expected (M.S.)
Total	204		
Years	4	4,207.664	
Breeds in years	7	42.030	
Sires in breeds	30	3.651	$\sigma_e^2 + 4.289 \sigma_s^2$
Daughters in sires	163	9.697	σ_e^2

*Ayrshire, Guernsey, Holstein and Jersey.

TABLE XXII

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF STABLE FLY
SUSCEPTIBILITY IN AYRSHIRES

Source	d.f.	M.S.	Expected (M.S.)
Total	53		
Years	2	473.349	
Sires in years	8	8.180	$\sigma_e^2 + 4.517 \sigma_s^2$
Daughters in sires	43	7.455	σ_e^2

TABLE XXIII

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF STABLE FLY
SUSCEPTIBILITY IN GUERNSEYS

Source	d.f.	M.S.	Expected (M.S.)
Total	29		
Years	1	.273	
Sires in years	4	.506	$\sigma_e^2 + 3.916 \sigma_s^2$
Daughters in sires	24	.467	σ_e^2

TABLE XXIV

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF STABLE FLY
SUSCEPTIBILITY IN HOLSTEINS

Source	d.f.	M.S.	Expected (M.S.)
Total	95		
Years	4	148.481	
Sires in years	9	2.722	$\sigma_e^2 + 6.395 \sigma_s^2$
Daughters in sires	82	3.224	σ_e^2

TABLE XXV

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF STABLE FLY
SUSCEPTIBILITY IN JERSEYS

Source	d.f.	M.S.	Expected (M.S.)
Total	24		
Years	1	12.799	
Sires in years	9	.845	$\sigma_e^2 + 2.145 \sigma_s^2$
Daughters in sires	14	.693	σ_e^2

TABLE XXVI

INTRA-YEAR, INTRA-BREED, INTRA-SIRE ANALYSIS OF VARIANCE OF
STABLE FLY SUSCEPTIBILITY IN ALL-BREEDS*

Source	d.f.	M.S.	Expected (M.S.)
Total	204		
Years	4	412.692	
Breeds in years	7	34.704	
Sires in breeds	30	3.319	$\sigma_e^2 + 4.289 \sigma_s^2$
Daughters in sires	163	3.717	σ_e^2

*Ayrshire, Guernsey, Holstein, and Jersey.

TABLE XXVII

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF HORN FLY
SUSCEPTIBILITY IN AYRSHIRES

Source	d.f.	M.S.	Expected (M.S.)
Total	53		
Years	2	5,869.675	
Sires in years	8	195.192	$\sigma_e^2 + 4.517 \sigma_s^2$
Daughters in sires	43	497.567	σ_e^2

TABLE XXVIII

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF HORN FLY
SUSCEPTIBILITY IN GUERNSEYS

Source	d.f.	M.S.	Expected (M.S.)
Total	29		
Years	1	1,108.785	
Sires in years	4	18.487	$\sigma_e^2 + 3916 \sigma_s^2$
Daughters in sires	24	9.372	σ_e^2

TABLE XXIX

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF HORN FLY
SUSCEPTIBILITY IN HOLSTEINS

Source	d.f.	M.S.	Expected (M.S.)
Total	95		
Years	4	7,573.724	
Sires in years	9	350.313	$\sigma_e^2 + 6.395 \sigma_s^2$
Daughters in sires	82	261.691	σ_e^2

TABLE XXX

INTRA-YEAR, INTRA-SIRE ANALYSIS OF VARIANCE OF HORN FLY
SUSCEPTIBILITY IN JERSEYS

Source	d.f.	M.S.	Expected (M.S.)
Total	24		
Years	1	201.531	
Sires in years	9	127.220	$\sigma_e^2 + 2.145 \sigma_s^2$
Daughters in sires	14	46.384	σ_e^2

TABLE XXXI

INTRA-YEAR, INTRA-BREED, INTRA-SIRE ANALYSIS OF VARIANCE OF
HORN FLY SUSCEPTIBILITY IN ALL-BREEDS*

Source	d.f.	M.S.	Expected (M.S.)
Total	204		
Years	4	11,600.156	
Breeds in years	7	438.172	
Sires in breeds	30	197.776	$\sigma_e^2 + 4.289 \sigma_s^2$
Daughters in sires	163	268.272	σ_e^2

*Ayrshire, Guernsey, Holstein and Jersey.

APPENDIX B

TABLE XXXII

THE BREAKDOWN OF HALF-SIBS WITHIN SIRE OF EACH BREED
FOR THE VARIOUS YEARS

Breed	Sire Number	1953	1954	1957	1958	1959
Ayrshire	1	7	9	-	-	2
	2	3	9	-	-	2
	3	5	3	-	-	-
	4	4	2	-	-	-
	5	-	-	-	-	6
Guernsey	1	13	-	-	-	-
	2	6	-	-	-	5
	3	-	-	-	-	3
	4	-	-	-	-	2
	5	-	-	-	-	1
Holstein	1	9	8	-	-	-
	2	7	9	9	10	9
	3	4	7	9	7	5
	4	-	-	-	-	3
	5	-	-	-	-	2
Jersey	1	5	-	-	-	2
	2	5	-	-	-	-
	3	3	-	-	-	1
	4	3	-	-	-	1
	5	-	-	-	-	2
	6	-	-	-	-	1
	7	-	-	-	-	1
	8	-	-	-	-	1

-No daughters counted.

APPENDIX C

TABLE XXXIII

VARIANCES AND COVARIANCES OF HOUSE FLY, STABLE FLY, AND HORN FLY SUSCEPTIBILITY
FOR UNRELATED PAIRS OF EACH BREED

Breed	House Fly			Stable Fly			Horn Fly		
	Variances		Covariance	Variances		Covariance	Variances		Covariance
Ayrshire	52.6	48.4	5.5	3.5	7.2	-.5	280.8	315.5	9.9
Guernsey	44.2	115.2	13.2	.9	1.6	.2	70.5	90.5	2.8
Holstein	782.3	1046.3	-68.6	52.8	59.6	-3.0	698.8	715.1	220.5
Jersey	1403.8	42.9	-157.4	2.4	2.3	-.8	361.2	73.8	6.1
All-breeds*	783.4	730.4	140.1	62.5	54.7	31.5	549.5	631.3	259.9

*Above breeds combined to form one group.

TABLE XXXIV

VARIANCES AND COVARIANCES OF HOUSE FLY, STABLE FLY, AND HORN FLY SUSCEPTIBILITY
FOR DAM-DAUGHTER PAIRS OF EACH BREED

Breed	House Fly			Stable Fly			Horn Fly		
	Variance			Variance			Variance		
	Dam	Daughter	Covariance	Dam	Daughter	Covariance	Dam	Daughter	Covariance
Ayrshire	12.9	141.8	16.8	2.1	3.2	.6	220.1	542.5	82.4
Guernsey	1.6	136.0	2.4	.4	1.5	-.2	16.9	99.1	12.7
Holstein	898.8	2179.9	-26.5	207.2	69.7	-8.0	849.2	622.6	101.2
Jersey	639.5	915.5	-339.0	1.7	5.0	1.5	103.2	194.5	74.7
All-breeds*	3067.7	1462.2	407.7	103.9	57.6	35.5	759.3	501.8	196.9

*Above breeds combined to form one group.

APPENDIX D

TABLE XXXV

AGE, SKIN THICKNESS, WHITE-SPOTTING AND AVERAGE HOUSE FLY, STABLE FLY AND HORN FLY COUNTS OF AYRSHIRE COWS

Cow Number	Age in Months	Skin Thickness*	White-spotting**	House Fly	Stable Fly	Horn Fly
134	66	.283	95.0	.00	1.31	7.09
139	81	.287	10.0	.09	4.12	31.19
144	92	.347	100.0	.00	1.66	4.34
145	90	.307	95.0	.00	1.91	11.91
148	78	.304	57.5	.00	.97	9.78
149	58	.292	45.0	.12	3.69	14.06
151	80	.290	15.0	.00	3.87	13.81
152	80	.302	100.0	.00	2.62	45.44
155	52	.272	97.0	.03	1.34	6.16
157	99	.259	25.0	.00	2.00	12.87
158	34	.296	91.0	.00	.72	4.22
159	53	.297	98.5	.00	2.53	7.69
162	65	.289	15.0	.19	4.81	22.06
165	55	.333	95.0	.00	1.53	9.44
169	81	.316	98.5	.03	1.28	3.62
176	109	.291	20.0	.06	3.97	13.87
178	40	.285	97.0	.00	1.12	10.66
179	36	.304	98.0	.00	.94	2.31

*Double layer in inches.

**Percentage.

TABLE XXXVI
 AGE, SKIN THICKNESS AND AVERAGE HOUSE FLY, STABLE FLY, AND
 HORN FLY COUNTS OF GUERNSEY COWS

Cow Number	Age in Months	Skin Thickness*	House Fly	Stable Fly	Horn Fly
1	90	.255	.27	4.60	6.33
3	46	.290	.07	3.23	13.10
4	78	.254	.53	4.17	12.16
6	41	.274	.17	3.00	6.87
8	36	.278	.13	2.47	4.83
9	103	.259	.33	3.87	6.87
11	48	.248	.53	3.27	10.10
13	40	.270	.47	3.17	8.27
14	63	.312	.30	1.90	9.23
15	47	.312	.17	3.07	6.33
16	45	.251	.20	2.63	10.60
17	73	.283	.17	1.47	3.63
22	41	.238	.20	1.83	14.13
23	36	.254	.77	5.03	14.16
27	70	.318	.20	2.43	6.70
36	76	.266	.07	1.40	8.40
37	36	.269	.33	3.33	4.27
38	33	.265	.27	3.50	6.70
39	115	.265	.07	2.50	6.20

*Double layer in inches.

TABLE XXXVII

AGE, SKIN THICKNESS AND AVERAGE HOUSE FLY, STABLE FLY, AND
HORN FLY COUNTS OF JERSEY COWS

Cow Number	Age in Months	Skin Thickness*	House Fly	Stable Fly	Horn Fly
102	83	.230	.16	4.87	32.81
109	88	.257	.06	5.26	11.03
110	85	.255	.00	2.26	10.68
112	81	.206	.16	3.29	26.58
114	45	.247	.06	3.32	23.32
121	59	.264	.10	2.45	10.16
124	40	.249	.00	3.77	11.32
125	52	.219	.00	4.68	25.52
126	37	.255	.00	1.29	16.07
127	106	.245	.00	3.64	26.74
128	103	.232	.10	3.74	16.65
138	35	.261	.00	2.52	17.87

*Double layer in inches.

TABLE XXXVIII

AGE, SKIN THICKNESS, WHITE-SPOTTING AND AVERAGE HOUSE FLY, STABLE FLY, AND HORN FLY COUNTS OF HOLSTEIN COWS

Number	Age in Months	Skin Thickness*	White-spotting**	House Fly	Stable Fly	Horn Fly
39	45	.281	72.5	.31	3.27	14.69
40	90	.274	57.5	.35	2.58	10.50
42	51	.249	99.0	.08	.69	2.50
43	141	.296	19.0	.42	4.27	19.31
44	68	.261	93.5	.54	1.65	5.12
45	75	.294	14.5	.31	3.31	11.96
46	75	.249	47.5	.42	2.69	10.61
48	47	.239	56.5	.27	2.77	3.40
50	34	.279	66.5	.08	2.08	4.69
56	105	.304	72.5	.19	5.08	11.04
58	117	.286	2.0	.73	6.85	25.65
59	69	.297	2.0	.73	6.69	25.58
62	76	.297	42.5	.15	3.08	7.58
64	61	.223	6.5	.08	3.65	13.69
65	55	.281	52.5	.35	3.19	10.42
67	108	.279	82.5	.50	1.73	6.12
70	48	.259	92.0	.15	.96	4.19
74	53	.281	52.5	.27	4.85	22.11
77	97	.273	95.0	.23	2.38	6.54
81	116	.270	93.5	1.96	4.77	4.42
82	74	.280	89.0	.35	1.42	4.23
85	58	.279	22.5	1.31	3.46	13.54
87	62	.256	7.5	.31	3.85	23.42
89	96	.238	49.5	.38	2.04	9.23
91	138	.256	60.0	.15	3.96	7.15
92	125	.265	20.0	.54	4.31	15.77
93	45	.257	37.5	.50	2.73	14.65
94	129	.257	11.0	2.04	7.19	38.42
95	81	.252	20.5	1.42	3.81	16.35
98	53	.279	55.0	.38	3.27	12.38
99	109	.232	5.0	.47	7.85	17.77
103	50	.293	12.5	1.92	3.20	12.19
100	57	.331	99.5	.04	1.19	4.65
113	47	.302	98.0	.12	1.38	3.31

*Double layer in inches.

**Percentage.

APPENDIX E

TABLE XXXIX

CORRECTED SUMS OF SQUARES AND CROSS PRODUCTS FOR AGE, WHITE-SPOTTING, SKIN THICKNESS
AND FLY SUSCEPTIBILITY OF AYRSHIRE COWS

	Skin Thickness				White- spotting	House Fly	Stable Fly	Horn Fly	Age
	Escutcheon	Side	Neck	Total					
Escutcheon	.015	.005	.006	.027	6.257	-.007	-.123	-.242	2.174
Side	.005	.015	.006	.026	6.405	-.002	-.034	-1.738	-1.555
Neck	.006	.006	.008	.021	8.008	-.008	-.156	-.611	-1.262
Total	.027	.026	.021	.074	20.670	-.016	-.313	-2.591	-.643
White- spotting	6.257	6.405	8.008	20.670	22935.625	-19.968	-637.051	-2360.420	-6184.583
House Fly	-.007	-.002	-.008	-.016	-19.968	.049	.878	3.152	1.048
Stable Fly	-.123	-.034	-.156	-.313	-637.051	.878	28.591	135.197	189.163
Horn Fly	-.242	-1.738	-.611	-2.591	-2360.425	3.152	135.196	1961.154	1201.513
Age	2.174	-1.555	-1.262	-.643	-6184.583	1.048	189.163	1201.513	8120.280

TABLE XL

CORRECTED SUMS OF SQUARES AND CROSS PRODUCTS FOR AGE, SKIN THICKNESS AND
FLY SUSCEPTIBILITY OF GUERNSEY COWS

	Skin Thickness			Total	House Fly	Stable Fly	Horn Fly	Age
	Escutcheon	Side	Neck					
Escutcheon	.001	.007	.002	.193	-.030	-.230	-.501	1.512
Side	.007	.033	.004	.040	-.040	-.287	-.732	-2.845
Neck	.002	.004	.004	.012	-.009	-.001	-.279	-.700
Total	.019	.040	.012	.080	-.068	-.404	-2.058	-.058
House Fly	-.030	.040	-.009	-.068	.572	2.257	7.062	-20.310
Stable Fly	-.230	-.287	-.001	-.404	2.257	17.738	20.290	-12.890
Horn Fly	-.501	-.732	-.279	-2.058	7.062	20.290	251.334	-171.010
Age	1.512	-2.845	-.670	-.058	-20.310	-12.890	-171.010	10744.50

TABLE XLI

CORRECTED SUMS OF SQUARES AND CROSS PRODUCTS FOR AGE, WHITE-SPOTTING, SKIN THICKNESS,
AND FLY SUSCEPTIBILITY OF HOLSTEIN COWS

	Skin Thickness				White- spotting	House Fly	Stable Fly	Horn Fly	Age
	Escutcheon	Side	Neck	Total					
Escutcheon	.024	.008	.011	.038	.801	-.044	.115	.684	-6.040
Side	.008	.048	.013	.075	14.850	.085	-.330	-.870	.356
Neck	.011	.013	.056	.047	6.708	-.097	.040	-1.894	16.216
Total	.038	.075	.047	.169	19.980	.013	-.295	-1.065	-1.791
White-spotting	.801	14.850	6.708	19.980	39500.642	-170.080	-1361.298	-6831.934	-5994.714
House Fly	-.044	.085	-.097	.013	-170.080	10.109	12.821	58.606	152.328
Stable Fly	.115	-.330	.040	-2.952	-136.130	12.821	104.971	376.489	920.656
Horn Fly	.684	-.870	-1.894	-1.065	-6831.934	58.606	376.489	2137.062	2570.323
Age	-6.040	.356	16.216	-1.791	-5994.714	152.328	920.656	2570.323	31604.970

TABLE XLII

CORRECTED SUMS OF SQUARES AND CROSS PRODUCTS FOR AGE, SKIN THICKNESS, AND
FLY SUSCEPTIBILITY OF JERSEY COWS

	Skin Thickness				House Fly	Stable Fly	Horn Fly	Age
	Escutcheon	Side	Neck	Total				
Escutcheon	.004	.002	.001	.007	-.002	-.166	-.570	.073
Side	.002	.011	.003	.017	-.014	-.041	-2.530	-2.279
Neck	.001	.003	.004	.008	-.003	-.083	-1.197	-2.380
Total	.007	.012	.008	.032	-.019	-.290	-4.297	-4.586
House Fly	-.002	-.014	-.003	-.019	.044	.248	3.111	7.007
Stable Fly	-.166	-.041	-.083	-.290	.248	15.009	34.559	133.508
Horn Fly	-.570	-2.530	-1.197	-4.297	3.111	34.559	896.478	567.552
Age	.073	-2.279	-2.380	-4.586	7.007	133.508	567.552	7451.670

TABLE XLIII

CORRECTED SUMS OF SQUARES AND CROSS PRODUCTS FOR AGE, WHITE-SPOTTING, SKIN THICKNESS,
AND FLY SUSCEPTIBILITY OF ALL-BREEDS*

	Skin Thickness				White- spotting	House Fly	Stable Fly	Horn Fly	Age
	Escutcheon	Side	Neck	Total					
Escutcheon	.081	.046	.035	.158	-21.750	-.256	-1.072	-1.932	-4.548
Side	.046	.142	.050	.244	27.190	.053	-1.246	-9.648	-4.475
Neck	.035	.050	.087	.142	17.990	-.085	-.529	-6.405	13.575
Total	.158	.244	.142	.562	61.350	-.247	-2.901	-16.982	-5.789
White- spotting	-21.750	27.190	17.990	61.350	67577.790	-309.480	-2287.20	-33917.290	-14103.300
House Fly	-.256	.053	-.085	-.247	-309.480	14.398	21.744	47.132	205.183
Stable Fly	-1.072	-1.246	-.529	-2.901	-2287.200	21.744	184.344	596.148	1333.318
Horn Fly	-1.932	-9.648	-6.405	-16.980	-33917.290	47.132	596.148	6200.702	4653.347
Age	-4.548	-4.475	13.575	-5.780	-14103.300	205.183	1333.308	4653.347	61761.470

*Ayrshire, Guernsey, Holstein and Jersey.

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