Transformation of Measurements Percentage of White Coat Color for Holsteins and Estimation of Heritability[1]

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ABSTRACT

Percentage of white coat color was measured on registration certificates of 4293 Holstein heifers on eight dairy farms in Florida. Measurements of white percentage were by visual evaluation on one side of the upper body (head, neck, and trunk) only and obtained in increments of 5%. Mean, median, mode, standard deviation, and skewness of white percentage were 25.6, 15, 0, 26.9, and 1.03. Distribution of white percentages showed lack of normality. Original data were transformed using an extension of the Box-Cox transformation to approach normality and to provide maximum likelihood estimators of the transformed parameters. Heritability estimates for percentages of white coat color were computed using derivative-free REML with an animal model. Estimates of heritability were .715 from untransformed data and .779 for transformed. Standard errors of estimates were slightly lower (.032 vs. .035) following transformation. Additional study to find an improved transformation procedure still seems warranted.

(**Key words**: coat color, heritability, Holstein)

Abbreviation key: WP = Percentage of white coat color.

INTRODUCTION

In a subtropical environment, the percentage of white coat color (WP) of Holsteins affects production and perhaps reproduction; for example, the regression of milk yield on WP was 1.91 kg (4).

Statistical properties, distribution, and heritability of WP of Holsteins have been estimated from single herds and small data files [<800 observations; (2, 3, 5, 6)]. The WP mean, standard deviation, and coefficient of variation from total bodies of cows have ranged from 27.8 to 56.7, 20.8 to 29.6, and 47 to 75 (3, 5, 6). Briquet and Lush (5) reported a nearly rectangular and symmetrical frequency distribution of WP. Becerril and Wilcox (3) recorded WP from the upper body (head, neck, and trunk) of cows and found estimates of 17.7 and 21.6 for mean and standard deviation, along with a nonsymmetric frequency distribution skewed to the right. The upper body should be more sensitive to the possible detrimental effects of heat stress caused by absorption of solar radiation in a subtropical environment than the lower body, and upper body measurements are easier to record.

Lack of Normality

Measurements that represent a percentage, such as WP, often follow a nonnormal distri-

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bution. Nonnormality has been mentioned as a possible source of error when variance components and genetic parameters are estimated (1, 16). Currently, REML with an animal model is the method most preferred in animal breeding to estimate genetic parameters. Derivations from REML depend on the assumption that the response variable follows a multivariate normal distribution. If no attention is paid to how the trait under study is distributed, and it is analyzed using REML, the possibility exists of violating some statistical properties that REML estimates are supposed to have. Although Harville (10) mentioned that REML estimators derived under the assumption of normality are reasonable (minimum variance) even when the distribution of the random effects in a mixed model are unspecified, Banks et al. (1) empirically studied robustness of REML as a tool for estimation of variance components and heritability, applied to data with skewed distributions. They (1) used a one-way random sire model and found that REML was robust for expectations, but not for sampling variances of the estimate, resulting in larger estimates in skewed distributions. Westfall (16) studied covariance matrices with large samples for different estimation methods (ANOVA, minimum quadratic unbiased estimator, maximum likelihood, and REML) of variance components for the unbalanced one-way model when the underlying distributions were not normal, and he pointed out that the limiting (asymtotic) variances depended on the design sequence, on the actual values of the variance components, and on the kurtosis (not skewness) parameters of the underlying distributions. Although theoretical considerations support the use of REML despite data distribution, empirical evidence suggests that the variances of REML estimates could be affected by nonnormality.

Transformation

To approach normality for WP, empirical transformations (arcsin, square root, log) have been used with little success to date (5). The Box-Cox power transformation has been used in fixed effects models in which observations are nonnegative. Spitzer (15) presented a lucid explanation of the Box-Cox power transformation for fixed effects models, which was extended later to random balanced models by Solomon (14) and, more recently, to mixed models (with relationships among individuals included) following a Bayesian approach by Gianola et al. (7). Although WP is a continuous variable, measurements, as pointed out, were approximations grouped in intervals of 5%. Guerrero and Johnson (9) extended the Box-Cox transformation theory to grouped data of a single random variable. The computing program for the [Guerrero and Johnson (9)] transformation permits analysis of grouped and ungrouped data and was used in our research to transform WP.

Heritability of Coat Color

Inheritance of coat color of Holsteins apparently was studied first by Dunn et al. (6). The three estimates of heritability they computed from intrasire regression of offspring on dam averaged .52. Later, Briquet and Lush (5) measured WP and estimated heritabilities of .99 and .93 from intrasire regression of offspring on dam and regression of offspring on midparent. They concluded that the heritability of this trait was very high and that little nonadditive variation occurred. More recently, King et al. (12) used a paternal half-sib model to estimate heritability by ANOVA-like methods. Cows were grouped into three categories (white, mixed, and black). No mathematical model was presented. The heritability estimate of .22 was considerably smaller than other estimates, perhaps as a consequence of the gross scale used. Becerril et al. (2) estimated heritability of .91 for WP using a paternal half-sib model and also a method similar to ANOVA.

Thus, evidence suggests that heritability of coat color is high, at least when measured on a continuous scale. To date, no studies have been conducted on data files for several herds from the field using current statistical techniques that take advantage of modern computing capabilities. For example, no reports were found of heritability estimates using REML with an animal model for coat color. Objectives of our research were to estimate statistical properties and the empirical distribution of WP, using a large data file from several herds, and to examine another transformation of WP to estimate its heritability with REML from transformed and untransformed data.

MATERIALS AND METHODS

Data

Measurements of WP, as described by Becerril and Wilcox (3), were obtained by visual evaluations of cow drawings on 4293 registration certificates. The registration certificates were from eight herds located in northern and central Florida and were obtained mainly on the farm and also from the Holstein Association of America. Measurements of WP were taken in increments of 5% and grouped into 21 classes by a single evaluator. Correlations between visual evaluations and measurements taken on a continuous scale by a planimeter were higher than .97 (3). Pedigree information since 1950 of the cows with WP evaluations were provided by the USDA and the Holstein Association of America.

Mathematical Model

The distribution function of WP measurements is unknown, although empirical evidence has shown lack of normality. Because REML procedures have been developed assuming normality, we hoped that a suitable transformation of WP would allow construction of a model for analysis for our own data that could be expressed as

$$y_i = \mu + a_i + e_i \qquad [1]$$

where y_i = transformed WP of cow i ($i = 1,2,\ldots; n = 4293$), μ = overall mean, a_i = additive genetic effect of cow i, and e_i = residual effect.

Assumptions are that the model is specified correctly and that a_i are identically distributed normal variables ~ idn $(0, \sigma_a^2)$, e_i are independent and identically distributed normal variables ~ iidn $(0, \sigma_e^2)$, where σ_a^2 is the additive variance, σ_e^2 is the residual variance, and $\text{cov}(a_i, e_i) = 0$. Cows are related, $\text{cov}(a_i, a_j) = c_{ij}\,\sigma_a^2$ for $i \neq j$, where c_{ij} is the additive genetic relationship between cows i and j.

The only fixed effect in the model is the mean, and animals and residuals are random effects. No empirical evidence suggests that any other fixed effects on WP exist. Herd effects could exist, however, with drawings if those preparing the drawings erred systematically.

Model [1] may be expressed using matrix notation as

$$\mathbf{y} = \mathbf{1}\mu + \mathbf{Za} + \mathbf{Ie} \qquad [2]$$

where **y** is an N × 1 vector of WP observations, N is the total number of cows with measurements, μ is the constant mean, **a** is an N × 1 vector of additive values for individual cows, **e** is an N × 1 vector of residuals, **1** is the N × 1 vector for which entries all are ones, **Z** is the N × N incidence matrix for animal effects, and **I** is the identity matrix. First and second moments are defined as

$$E\begin{bmatrix}\mathbf{y}\\ \mathbf{a}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{1}\mu\\ 0\\ 0\end{bmatrix}$$

$$\text{Var}\begin{bmatrix}\mathbf{y}\\ \mathbf{a}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{ZGZ'+R} & \mathbf{GZ'} & \mathbf{R}\\ \mathbf{GZ'} & \mathbf{G} & 0\\ \mathbf{R} & 0 & \mathbf{R}\end{bmatrix}$$

where $\mathbf{G} = \mathbf{A}\sigma_a^2$, **A** = additive relationship matrix, and $\mathbf{R} = \mathbf{I}\sigma_e^2$. Normality is assumed to hold for **a** and **e**. With only registered cows in the data, few unknown ancestors were found, including those without records.

For Model [2], the mixed model equations are

$$\begin{bmatrix}N & \mathbf{1}'\\ \mathbf{1} & \mathbf{I}+\mathbf{A}^{-1}\nu\end{bmatrix}\begin{bmatrix}\hat{\mu}\\ \hat{\mathbf{a}}\end{bmatrix} = \begin{bmatrix}\mathbf{1}'\mathbf{y}\\ \mathbf{y}\end{bmatrix} \qquad [3]$$

with $\nu = \sigma_e^2/\sigma_a^2$, and other elements are defined as before. Transformed and original data were analyzed using Model [3]. Estimates from REML of σ_a^2 and σ_e^2 were obtained by a derivative-free method. Theory and computational methods were given by Graser et al. (8) and Meyer (13).

The Guerrero and Johnson Transformation

Maximum likelihood estimates of the mean (μ), phenotypic standard deviation (σ), and the power transformation parameter (λ) were calculated. The procedure assumed that WP measurements represented a random sample

TABLE 1. Descriptive statistics for percentage for herds and overall data.

Herd	n	Mean	SD	CV	Median	Maximum	Skewness
1	170	34.0	29.8	87	30	95	.39
2	1026	29.7	27.7	93	20	100	.80
3	1084	25.3	26.3	104	15	100	1.03
4	1047	20.8	24.7	118	10	100	1.40
5	464	24.8	26.7	107	15	100	1.14
6	92	30.6	30.7	100	20	100	.94
7	173	27.2	26.4	97	20	95	.86
8	237	24.1	28.2	117	10	100	1.18
Total	4293	25.6	26.9	105	15	100	1.03[1]

[1] Overall test of skewness was significant (*P* < .01).

$X_1, X_2, \ldots, X_n$ taken from a continuous distribution. Measurements of WP were approximations obtained by visual evaluations and were grouped in 21 intervals of 5% denoted by

$$D_1 = [b_0, b_1),$$
$$D_2 = [b_1, b_2), \ldots,$$
$$D_k = [b_{k-1}, b_k)$$

where

$$0 = b_0 < b_1 < b_2 < \ldots b_{k-1} < b_k = \infty.$$

The total sample is denoted by $N = \Sigma n_i = 4293$, where n_i is the number of observations in each interval D_i. To obtain maximum likelihood estimates of μ, σ, and λ, a λ_o was presumed to exist such that

$$X_j^{(\lambda_o)} = \left\{ \begin{array}{l} \dfrac{X_j^{\lambda_o} - 1}{\lambda_o}, \ \lambda_o \neq 0 \\ \log (X_j), \ \lambda_o = 0 \end{array} \right\}$$

has a normal distribution. Under this assumption, with $\lambda \geq 0$,

$$P[X_1 \epsilon D_i] = P[b_{i-1} \leq X_1 < b_i]$$

$$= P\left[\frac{b_{i-1}^{\lambda} - 1}{\lambda} \leq \frac{X_1^{\lambda} - 1}{\lambda} < \frac{b_i^{\lambda} - 1}{\lambda}\right]$$

$$= \Phi\left(\frac{b_i^{(\lambda)} - \mu}{\sigma}\right) - \Phi\left(\frac{b_{i-1}^{(\lambda)} - \mu}{\sigma}\right)$$

$$= p_i(\mu, \sigma, \lambda)$$

where

$$b_i^{(\lambda)} = \left\{ \begin{array}{l} \dfrac{b_i^{\lambda} - 1}{\lambda}, \ \lambda \neq 0 \\ \log (b_i), \ \lambda = 0 \end{array} \right\}$$

for $i = 1,2,\ldots,k-1$, and Φ represents the standard normal cumulative distribution function. For $i = 0,k$

$$P_0 \ (\mu, \sigma, \lambda) = \Phi\left(\frac{b_1^{(\lambda)} - \mu}{\sigma}\right)$$

and

$$P_r \ (\mu, \sigma, \lambda) = 1 - \Phi\left(\frac{b_{k-1}^{(\lambda)} - \mu}{\sigma}\right),$$

for $\lambda \geq 0$.

Counts $(n_1, n_2, \ldots, n_k)$ then have a multinomial distribution, the probabilities of which are given by the p_i. The log-likelihood is maximized in two steps. First, λ is fixed and the log-likelihood is maximized for μ and σ; second, the partially maximized likelihood is maximized over λ [for a detailed description see Guerrero and Johnson (9)].

RESULTS AND DISCUSSION

Descriptive statistics of WP for each herd and overall data are in Table 1. For individual herds, data were not distributed uniformly. Three herds had 73.54% of the data, and one herd had only 2.14%. The means for WP by herd ranged from 20.8 to 34.0%. This range represented a difference of 63.5%. Two dairy

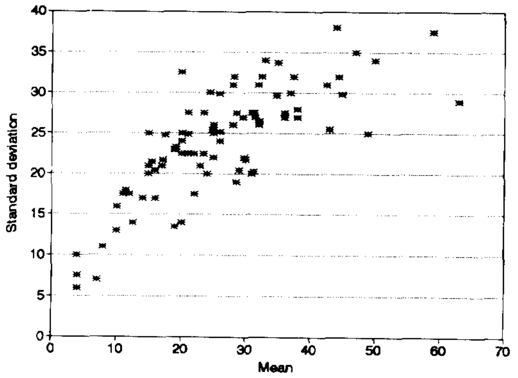

Figure 1. Relationship between means and standard deviations of sire progeny groups for percentage of white coat color.

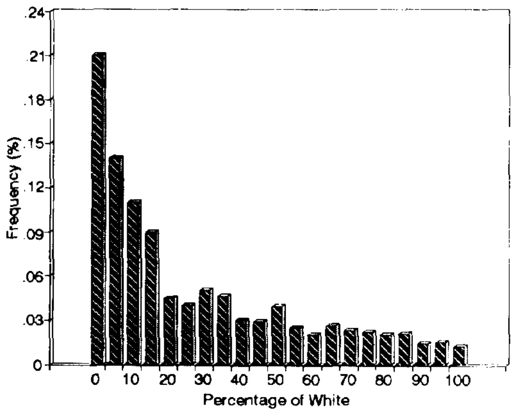

Figure 2. Distribution of percentages of white coat color (n = 4293).

producers indicated that they had personal preference for whiter sires. If selection for more white on the coat occurred, it occurred at the individual herd level. For all herds, mode was 0, and median was low. Only two herds had no cows that were all white. Estimates of variability within herds were large. Variability was associated with the mean; standard deviations tended to be larger and coefficients of variation smaller as the mean increased. The same trend was observed for sires with >10 daughters (Figure 1); i.e., variability among darker sire groups was lower than that among whiter sires. By herd, skewness values were all positive. Kurtosis ranged from −1.319 to 1.263. The overall mean, standard deviation, and coefficient of variation were 25.6, 26.9, and 105%. These values agreed closely with previous results obtained by Becerril et al. (2) using a smaller data file (n = 795) than the present one from a single experimental herd, with more years but the same type of recording. The mode was 0, and the median was 15.

Although our study included only registered cows and a relatively small number of herds, Holsteins appear to be more black than white; 50% of the cows had <15% white on their upper body (trunk, neck, and head). Solid white cows under our measurement system were possible, however (i.e., cows with <2.5% black). Frequencies for each of the observed WP are presented in Figure 2; frequencies of cows was clearly reduced as WP increased. The maximum frequency of 20.8% was observed at the zero mode, a considerable decrease from the median of 15%; <1% of cows reached the maximum of 100% white. This asymmetric L-shaped distribution skewed to the right (skewness = 1.03) was found previously for WP (2, 3); however, Briquet and Lush (5) used scored color estimates differently and reported that the measure was uniformly distributed. Recording WP on the upper body may lead to a greater proportion of black (3). Overall kurtosis was −.0009. The D test for nonnormality was significant ($P < .01$).

Frequencies of transformed WP are in Figure 3. Intervals were not equal after transformation, and each one was represented by its class mean. Strict normality was not achieved, but distribution was somewhat more symmetric. Maximum likelihood estimates of μ, σ, and λ for this distribution were 3.889, 2.979, and .26375. Coefficient of variation was 76.6%, which was lower than the 105% obtained from untransformed WP data, although the same trend observed with original data between mean and variability was present for sires with >10 daughters. Guerrero and Johnson (9) established strong consistency and asymptotic normality for the estimators calculated with their transformation.

Starting values used in computing REML estimates of heritability for WP and transformed WP were .22, .90, and .99. However, Hoeschele (11) proved that, for two variance component models, the likelihood function is always unimodal, which guarantees that a

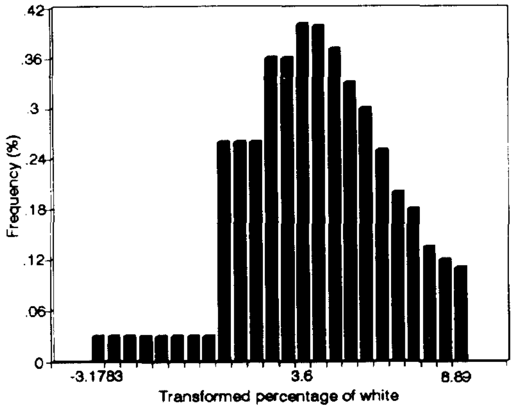

Figure 3. Distribution of transformed percentages of white color.

global maximum is obtained after convergence. In our study, the same heritability estimates were obtained regardless of starting values. The estimate of heritability for WP was high, .715 ± .035, which is larger than most other traits of dairy cattle, but smaller than .90 (2, 5). The standard error also was much smaller than previously reported (2, 5, 6). Our heritability estimate should be more reliable, because it was obtained from a larger data file from several herds in which additive relationships among individuals were considered, and because mixed model methodology was used.

Heritability of transformed WP was .779 ± .032, 9% larger than for WP. The estimate of its standard error was 6% less. In this case, transformation tended to increase heritability and to reduce its variability. To test for a significant difference between the two estimates of heritability, an estimate of covariance between them would be needed, but such information was not available. Banks et al. (1) found a larger dispersion of REML estimates of variance components when the underlying distribution was skewed. Westfall (16) mentioned that variance component estimates (minimum quadratic unbiased estimator, REML, and maximum likelihood) would have minimum variance only for null kurtosis, although he proved asymptotic normality for these estimates. The WP is an important trait for Holstein cows producing under adverse climatic conditions (4, 12), and, if its economic importance turns out to be large, a high heritability for this trait would be desirable if genetic correlations with other traits happen to be low and if correlated responses are important in a selection program. Under certain production conditions, this trait could become important.

CONCLUSIONS

The WP measured on the upper body from registration certificates of first lactation Holsteins was found to be a nonnormal variable skewed to the right. In our data, Holstein cows were mostly black with a mean WP of 25.6%; mode, 0; and median, 15. Variability in WP also was high; standard deviation was 26.9, and coefficient of variation was greater than 100%. The trait is highly heritable (.715 ± .035), higher than most other traits of dairy cattle. Transformation tended to result in an even larger estimate of heritability and a smaller standard error (.779 ± .032). Use of a transformation that normalizes WP may be desirable when variance components for the trait are estimated with REML procedures.

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