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L. Dale Van Vleck

University of Nebraska-Lincoln, dvan-vleck1@unl.edu

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Estimation of Heritability of Threshold Characters

L. D. VAN VLECK

Department of Animal Science
Cornell University, Ithaca, New York 14850

Abstract

Many traits of dairy cattle such as disease resistance and type breakdown scores may have an underlying distribution of values which are approximately normal but must be measured on a yes or no basis. Theory from literature suggests that heritability estimated from such binomial data is only $z^2/p(1-p)$ as large as heritability if it could be measured on the normal scale where z is the ordinate on the normal distribution at the threshold point corresponding to a fraction p of the population having the character. Data were generated from a pseudo-normal distribution to test this theory for estimates derived from parent-offspring correlation and paternal sib correlation. The adjustment from theory was quite satisfactory for the paternal sib correlation but would lead to substantial overestimates of heritability on the normal scale when p is small and normal heritability is actually large.

Introduction

The problem of estimating heritability from records classified as either one or zero arises frequently with characteristics such as type traits and disease resistance of dairy cattle. Such traits are likely to have an underlying continuous distribution of values but must be scored as a binomial variable. Several earlier papers [Lush, Lamoreux, and Hazel (4); Lush (3); Robertson and Lerner (5); and Dempster and Lerner with Robertson (1)] have considered this problem in general with particular reference to resistance to death in poultry. Their development has assumed an underlying normal distribution of genetic and environmental values with a linear relationship between the genetic value on the normal scale and the genetic value on the binomial scale. The theory suggests that heritability on the binomial scale is $h_b^2 = h^2 z^2 / [p(1-p)]$, where h^2 is heritability on the normal scale, z is the height of the ordinate of the normal distribution at the threshold point which determines whether the binomial variable is one or zero, and p is the frequency of ones.

Procedure

The theory was tested by generating samples of data with an underlying pseudo-normal distribution of genetic and environmental values; then truncating on phenotypic values corresponding to 10 probabilities of occurrence (5%, 10%, ..., 50%). The results should be interpreted noting that because of symmetry the results expected for probability of occurrence of 95% are the same as for 5%, etc. Heritabilities were then estimated from the binomial data (10 of these) and from the normal data.

Estimates from parent-offspring correlation were from 10,000 parent-offspring pairs with each parent having only one offspring. Two sets of 10 replicates each were generated for each of nine heritabilities (.1, .2, ..., .9). Average covariances and variances from each set of 10 replicates were used to compute average heritabilities which were little different from arithmetic averages. Estimates from paternal half-sib correlation were also from analyses of 10,000 records (100 sires with 100 progeny each). Average sire and error components of variance from each of two sets of 15 replicates were used to compute average heritabilities. Average heritability estimates for the normal data are in Table 1.

Results and Discussion

Difference from theory. Analysis of variance (Henderson, 2) of the difference between ratio of estimated binomial heritability to estimated normal heritability ($\overline{h_b^2/h^2}$) and $z^2/[p(1-p)]$ is shown in Table 2 with the two sets of average estimates assumed random and nested within method of estimation. This variable was chosen for analysis since the theoretical adjustment is proportional to the underlying normal heritability. The table shows the likelihood of real differences from theory due to method of estimating heritability, heritability, and threshold as well as of interactions among these.

Table 3 gives the averages which led to these significant differences. Over all thresholds and heritabilities parent-offspring estimates exceeded theoretical by .038 and paternal sib estimates exceeded theoretical by .016. In general, threshold had a greater effect on the difference of the

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TABLE 1. Average heritability estimates for normally distributed records by two methods of estimation.

Method of estimation	True heritability								
	.10	.20	.30	.40	.50	.60	.70	.80	.90
Parent-offspring	.101	.207	.295	.400	.497	.594	.704	.802	.900
Paternal sib	.093	.203	.303	.386	.516	.590	.714	.770	.917

parent-offspring estimates from theoretical than on paternal sib difference from theoretical although the average pattern was similar, i.e., there was greater under-estimation by theory at low frequencies of the trait than at frequencies near 50%. Similarly, the average estimates exceeded theoretical by more for high true heritability than for low heritability by both methods although the differences were greater for the parent-offspring method. These differences from theory were expected from results in the earlier papers which defined the differences as being due to the introduction of nonadditive genetic variance due to the change in scale from the normal to the binomial distribution.

Estimating heritability for data on the underlying normal scale by multiplying the binomial heritability by $p(1-p)/z^2$ appears to be a reasonable approach for the paternal sib method, at least for the design here. The validity of this approach is more doubtful for the parent-progeny method especially when only a small proportion of the population has the character. A reasonable approach would be to divide the binomial estimate of heritability by $z^2/p(1-p)$ plus a factor from Table 3 corresponding to p and a guessed value for normal heritability.

Expected progress from mass selection.

Dempster and Lerner (1) presented the procedure for calculating the change in the fraction of the population with the character by selection on the binomial scale when the character has an underlying normal scale. Let f be the fraction of the population selected to be parents. If $f \leq p$, the mean on the normal scale of the selected group will be z/p and the response by selection, $r = h^2z/p$. If $f > p$ the mean on the normal scale of the selected group will be the weighted average of those exhibiting the character and those not showing the character, $(p/f)(z/p) + [(f-p)/f] [-z/(1-p)] = [z(1-f)]/[f(1-p)]$ and $h^2[z(1-f)]/[f(1-p)]$ is the expected mean of the progeny on the normal scale. This will be less than the response expected if selection were on the normal scale which would be h^2z_f/f where z_f is the ordinate of the normal distribution corresponding to a fraction, f , selected. Since the original mean on the normal scale was zero, the progeny mean is the new population mean. The area between this mean and the threshold point can now be computed if the total variance has not changed. Rohlf and Sokal (6) list a computing formula which when corrected for some incorrect signs gives this area as

TABLE 2. Analysis of variance of $\bar{h}_b^2/\bar{h}^2 - z^2/p(1-p)$ where \bar{h}_b^2 and \bar{h}^2 are the average heritability estimates for the binomial and normal data for each set of replicates.

Source	DF	MS	F	Denominator	MS and DF
Method	1	.0441	34.34*	S M	2
Set Method	2	.0013	1.11	Synthesized	18.1
Heritability Level	8	.0113	11.26*	H × S M	16
M × H	8	.0021	2.10	H × S M	16
H × S M	16	.0010	3.51*	H × T × S M	144
Threshold Level	9	.0130	29.31*	T × S M	18
M × T	9	.0022	4.94*	T × S M	18
T × S M	18	.0004	1.55	H × T × S M	144
H × T	72	.0037	12.83*	H × T × S M	144
M × H × T	72	.0031	10.78*	H × T × S M	144
H × T × S M	144	.0003			

* ($P \leq .05$).

TABLE 3. Average differences from the expected binomial heritability for heritability estimated by parent-offspring correlation and paternal half-sib correlation, $\bar{h}_b^2/\bar{h}^2 - z^2/[p(1-p)]$.

Normal heritability	Per cent of population with character										Average
	5	10	15	20	25	30	35	40	45	50	
Parent-offspring correlation											
.10	.086	-.023	.034	-.159	-.118	-.030	-.109	.015	.156	.104	-.004
.20	.045	.091	-.040	.018	-.003	-.048	.007	.180	.112	.095	.046
.30	.052	.049	-.001	.029	.016	-.012	.106	.075	-.054	-.036	.022
.40	.038	.015	.048	.036	.024	.025	.064	-.011	-.060	-.012	.017
.50	.086	.055	.065	.098	.041	.038	-.008	-.084	-.016	.033	.031
.60	.115	.059	.071	.107	.047	.007	-.035	-.025	.047	.074	.047
.70	.116	.091	.079	.103	.024	.004	-.014	.012	.068	.077	.056
.80	.120	.096	.100	.086	.025	.010	.031	.051	.041	.023	.059
.90	.151	.134	.094	.086	.068	.043	.069	.062	-.014	-.002	.069
Average	.090	.063	.050	.045	.014	.004	.013	.031	.031	.040	.038
Paternal half-sib correlation											
.10	-.023	-.011	-.014	.000	-.019	-.018	.003	.004	.019	.029	-.003
.20	.043	.022	.026	.020	.016	.003	.005	.000	-.002	-.012	.012
.30	.014	.014	.015	.011	.018	.001	.001	.001	.002	.009	.009
.40	.035	.036	.027	.027	.011	.003	.003	.003	.004	.003	.015
.50	.036	.027	.022	.013	.001	-.006	-.001	-.003	.004	.005	.010
.60	.042	.036	.024	.022	.015	.010	.010	.011	.009	.011	.019
.70	.081	.070	.049	.035	.022	.014	.011	.006	.001	-.005	.028
.80	.040	.046	.038	.026	.016	.005	.004	.003	.008	.010	.020
.90	.079	.064	.050	.040	.030	.019	.019	.013	.010	.012	.034
Average	.039	.034	.026	.022	.012	.003	.006	.004	.006	.007	.016
z^2	.224	.342	.427	.489	.539	.579	.603	.622	.633	.636	
$p(1-p)$											

$$P(X) = .5 - \frac{d e^{-X^2/2}}{t(b_1 + t(b_2 + t(b_3 + t(b_4 + t b_5))))}$$

where X = original threshold value corresponding to $p - r$,

$$d = .3989423 = 1/\sqrt{2\pi},$$

$$t = 1/(1 + sX),$$

$$s = .2316419,$$

$$b_1 = .31938153,$$

$$b_2 = -.356553782,$$

$$b_3 = 1.781477937,$$

$$b_4 = -1.821255978, \text{ and}$$

$$b_5 = 1.330274429.$$

The expected fraction of the next generation with the character can be computed as $.5 - P(X)$ if $X > 0$ and $.5 + P(X)$ if $X \leq 0$ which converts selection on the normal scale back to the results in the binomial situation.

Tables 4a and 4b show these calculations for $h^2 = .1, .2, \dots, 1.0$; $p = .1, .2, \dots, .9$; and $f = .1, .2, \dots, .9$ whereas Dempster and Lerner (1) present a graph for $h^2 = .36, .64, 1.00$ and $f \leq p$ for $p = 0, \dots, 1.0$. They also present a graph of errors of estimating

gains on binomial heritabilities for various proportions selected for initial frequencies of the character of .05 and .5 for heritability on the normal scale of .36 and 1.00.

Gain predicted from binomial heritability. The binomial heritability, h_b^2 , can be used to predict the response on the binomial scale due to selection from heritability times the selection differential. When $f \leq p$, the selection differential is $(1-p)$ where animals with the character are assigned a value of one and others a value of zero. Thus, the predicted response is $h_b^2(1-p)$, and the predicted fraction of progeny showing the character is $p + h_b^2(1-p)$. If $f > p$, then the mean of the selected group is $[p(1) + (f-p)(0)]/f = p/f$, and the predicted response is $h_b^2(p/f-p)$. The predicted fractions of progeny showing the character using binomial heritability estimated as $h^2 z^2/[p(1-p)]$ are in Tables 5a and 5b for the same values of h^2, p , and f as for Table 4. Comparison with Table 4 shows that gain with a small fraction of progeny with the character will be underestimated and under-

TABLE 4a. Predicted per cent of next generation with desired characteristic with mass selection on the binomial scale (normal heritability = .1, .2, .3, .4, and .5).

Initial per cent	Per cent used as parents								
	10	20	30	40	50	60	70	80	90
Heritability on normal scale = .10									
10	13	11	11	11	10	10	10	10	10
20	24	24	22	21	21	21	20	20	20
30	34	34	34	33	32	31	31	30	30
40	44	44	44	44	43	42	41	41	40
50	53	53	53	53	53	52	51	51	50
60	62	62	62	62	62	62	62	61	60
70	72	72	72	72	72	72	72	71	70
80	81	81	81	81	81	81	81	81	80
90	90	90	90	90	90	90	90	90	90
Heritability on normal scale = .20									
10	18	13	12	11	11	10	10	10	10
20	29	29	25	23	22	21	21	20	20
30	38	38	38	35	34	32	31	31	30
40	48	48	48	48	45	43	42	41	41
50	56	56	56	56	56	54	53	52	51
60	65	65	65	65	65	65	63	62	61
70	73	73	73	73	73	73	73	72	71
80	82	82	82	82	82	82	82	82	81
90	91	91	91	91	91	91	91	91	91
Heritability on normal scale = .30									
10	22	15	13	12	11	11	10	10	10
20	34	34	28	25	23	22	21	21	20
30	43	43	43	38	35	34	32	31	31
40	51	51	51	51	48	45	43	42	41
50	59	59	59	59	59	56	54	52	51
60	67	67	67	67	67	67	65	63	61
70	75	75	75	75	75	75	75	73	71
80	83	83	83	83	83	83	83	83	81
90	91	91	91	91	91	91	91	91	91
Heritability on normal scale = .40									
10	28	17	14	12	11	11	11	10	10
20	39	39	30	26	24	23	22	21	20
30	48	48	48	41	37	35	33	32	31
40	55	55	55	55	50	47	44	43	41
50	63	63	63	63	63	58	55	53	51
60	70	70	70	70	70	70	66	64	62
70	77	77	77	77	77	77	77	74	72
80	84	84	84	84	84	84	84	84	82
90	91	91	91	91	91	91	91	91	91
Heritability on normal scale = .50									
10	34	19	15	13	12	11	11	10	10
20	44	44	33	28	25	23	22	21	21
30	52	52	52	44	39	36	34	32	31
40	59	59	59	59	53	48	45	43	41
50	66	66	66	66	66	60	57	54	52
60	72	72	72	72	72	72	68	65	62
70	78	78	78	78	78	78	78	75	72
80	85	85	85	85	85	85	85	85	82
90	92	92	92	92	92	92	92	92	92

TABLE 4b. Predicted per cent of next generation with desired characteristic with mass selection on binomial scale (normal heritability = .6, .7, .8, .9, and 1.0).

Initial per cent	Per cent used as parents									
	10	20	30	40	50	60	70	80	90	
Heritability on normal scale = .60										
10	41	21	16	13	12	11	11	11	11	10
20	50	50	36	30	26	24	23	21	21	21
30	57	57	57	47	41	37	35	33	31	31
40	63	63	63	63	55	50	47	44	42	42
50	68	68	68	68	68	63	58	55	52	52
60	74	74	74	74	74	74	69	65	62	62
70	79	79	79	79	79	79	79	76	73	73
80	85	85	85	85	85	85	85	85	83	83
90	92	92	92	92	92	92	92	92	92	92
Heritability on normal scale = .70										
10	48	23	17	14	13	12	11	11	10	10
20	55	55	39	32	28	25	23	22	21	21
30	61	61	61	50	43	38	35	33	31	31
40	66	66	66	66	58	52	48	44	42	42
50	71	71	71	71	71	65	59	56	52	52
60	76	76	76	76	76	76	71	66	63	63
70	81	81	81	81	81	81	81	77	73	73
80	86	86	86	86	86	86	86	86	83	83
90	92	92	92	92	92	92	92	92	92	92
Heritability on normal scale = .80										
10	55	26	18	15	12	12	11	11	10	10
20	61	61	42	34	29	26	24	22	21	21
30	66	66	66	53	45	40	36	34	32	32
40	70	70	70	70	60	54	49	45	42	42
50	74	74	74	74	74	66	61	56	53	53
60	78	78	78	78	78	78	72	67	63	63
70	82	82	82	82	82	82	82	78	73	73
80	87	87	87	87	87	87	87	87	83	83
90	92	92	92	92	92	92	92	92	92	92
Heritability on normal scale = .90										
10	62	28	19	15	13	12	11	11	10	10
20	66	66	46	36	30	26	24	22	21	21
30	70	70	70	56	47	41	37	34	32	32
40	73	73	73	73	63	55	50	46	43	43
50	76	76	76	76	76	68	62	57	53	53
60	80	80	80	80	80	80	73	68	64	64
70	83	83	83	83	83	83	83	78	74	74
80	88	88	88	88	88	88	88	88	84	84
90	93	93	93	93	93	93	93	93	93	93
Heritability on normal scale = 1.00										
10	68	31	20	16	14	12	12	11	10	10
20	71	71	49	38	31	27	24	23	21	21
30	74	74	74	59	49	42	38	34	32	32
40	76	76	76	76	65	57	51	46	43	43
50	79	79	79	79	79	70	63	58	54	54
60	82	82	82	82	82	82	75	69	64	64
70	85	85	85	85	85	85	85	79	74	74
80	88	88	88	88	88	88	88	88	84	84
90	93	93	93	93	93	93	93	93	93	93

TABLE 5a. Predicted per cent of next generation with desired characteristic using binomial selection differential and binomial heritability = $h^2z^2/p(1-p)$ [$h^2 = .1, .2, .3, .4, \text{ and } .5$].

Initial per cent	Per cent used as parents								
	10	20	30	40	50	60	70	80	90
Normal heritability = .10									
10	13	11	11	11	10	10	10	10	10
20	24	24	22	21	21	21	20	20	20
30	34	34	34	33	32	31	31	30	30
40	44	44	44	44	42	42	41	41	40
50	53	53	53	53	53	52	51	51	50
60	62	62	62	62	62	62	62	61	60
70	72	72	72	72	72	72	72	71	70
80	81	81	81	81	81	81	81	81	80
90	90	90	90	90	90	90	90	90	90
Normal heritability = .20									
10	16	13	12	11	11	10	10	10	10
20	28	28	25	23	22	21	21	20	20
30	38	38	38	35	33	32	31	31	30
40	47	47	47	47	45	43	42	41	41
50	56	56	56	56	56	54	53	52	51
60	65	65	65	65	65	65	63	62	61
70	73	73	73	73	73	73	73	72	71
80	82	82	82	82	82	82	82	82	81
90	91	91	91	91	91	91	91	91	91
Normal heritability = .30									
10	19	14	12	12	11	11	10	10	10
20	32	32	27	24	23	22	21	21	20
30	42	42	42	38	35	33	32	31	31
40	51	51	51	51	47	45	43	42	41
50	60	60	60	60	60	56	54	52	51
67	67	67	67	67	67	67	65	63	61
70	75	75	75	75	75	75	75	73	71
80	83	83	83	83	83	83	83	83	81
90	91	91	91	91	91	91	91	91	91
Normal heritability = .40									
10	22	15	13	12	11	11	11	10	10
20	36	36	29	26	24	23	22	21	20
30	46	46	46	40	37	35	33	32	31
40	55	55	55	55	50	47	44	42	41
50	63	63	63	63	63	58	55	53	51
60	70	70	70	70	70	70	66	64	62
70	77	77	77	77	77	77	77	74	72
80	84	84	84	84	84	84	84	84	82
90	91	91	91	91	91	91	91	91	91
Normal heritability = .50									
10	25	17	14	13	12	11	11	10	10
20	40	40	31	27	25	23	22	21	21
30	50	50	50	43	39	36	34	32	31
40	59	59	59	59	52	48	45	43	41
50	66	66	66	66	66	61	57	54	52
60	72	72	72	72	72	72	68	65	62
70	79	79	79	79	79	79	79	75	72
80	85	85	85	85	85	85	85	85	82
90	92	92	92	92	92	92	92	92	92

TABLE 5b. Predicted per cent of next generation with desired characteristic using binomial selection differential and binomial heritability = $h^2z^2/p(1-p)$ [$h^2 = .6, .7, .8, .9, \text{ and } 1.0$].

Initial Per cent	Per cent used as parents								
	10	20	30	40	50	60	70	80	90
Normal heritability = .60									
10	28	18	15	13	12	11	11	11	10
20	43	43	34	29	26	24	23	21	21
30	54	54	54	46	40	37	34	33	31
40	62	62	62	62	55	50	46	44	42
50	69	69	69	69	69	63	58	55	52
60	75	75	75	75	75	75	70	66	62
70	80	80	80	80	80	80	80	76	73
80	86	86	86	86	86	86	86	86	83
90	92	92	92	92	92	92	92	92	92
Normal heritability = .70									
10	32	20	16	14	12	12	11	11	10
20	47	47	36	30	27	25	23	22	21
30	58	58	58	48	42	38	35	33	31
40	66	66	66	66	57	52	47	44	42
50	72	72	72	72	72	65	60	56	52
60	77	77	77	77	77	77	71	67	63
70	82	82	82	82	82	82	82	77	73
80	87	87	87	87	87	87	87	87	83
90	92	92	92	92	92	92	92	92	92
Normal heritability = .80									
10	35	21	16	14	13	12	11	11	10
20	51	51	38	32	28	25	23	22	21
30	62	62	62	51	44	39	36	33	32
40	70	70	70	70	60	53	49	45	42
50	75	75	75	75	75	67	61	56	53
60	80	80	80	80	80	80	73	67	63
70	84	84	84	84	84	84	84	78	74
80	88	88	88	88	88	88	88	88	83
90	93	93	93	93	93	93	93	93	93
Normal heritability = .90									
10	38	22	17	15	13	12	11	11	10
20	55	55	41	33	29	26	24	22	21
30	66	66	66	53	46	40	37	34	32
40	74	74	74	74	62	55	50	46	42
50	79	79	79	79	79	69	62	57	53
60	82	82	82	82	82	82	74	68	64
70	86	86	86	86	86	86	86	79	74
80	89	89	89	89	89	89	89	89	84
90	93	93	93	93	93	93	93	93	93
Normal heritability = 1.00									
10	41	24	18	15	13	12	11	11	10
20	59	59	43	35	30	27	24	22	21
30	70	70	70	56	47	42	37	34	32
40	77	77	77	77	65	57	51	46	43
50	82	82	82	82	82	71	64	58	54
60	85	85	85	85	85	85	76	69	64
70	87	87	87	87	87	87	87	80	74
80	90	90	90	90	90	90	90	90	84
90	93	93	93	93	93	93	93	93	93

estimated more as h^2 increases. At high h^2 and $p \cong .5$ selection response will be slightly overestimated from the binomial data.

Conclusions

Heritability on the normal scale generally will be only slightly overestimated by multiplying the estimate from the paternal sib correlation from binomial data by $p(1-p)/z^2$ but may be overestimated substantially if the estimate from parent-offspring correlation is similarly adjusted particularly when p is not between .25 and .75. The overestimate will be greater when normal heritability is large than when it is small.

Genetic gain from mass selection as measured by the fraction of the population with the character will be underestimated when only a small fraction of the population has the character and when heritability on the normal scale is high as has been previously shown (1).

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