Modification of Beta-binomial Method of Estimation of Heritability of Stayability

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SUMMARY

Stayability, being an all-or-none trait in dairy cattle breeding, is one of the important characteristics and needs an indepth study of its inheritance. The modification in the beta-binomial method along with its comparison with other methods is being done for the estimation of heritability of this stayability. For illustration purpose, different data sets with varying levels of unbalancedness have been simulated and results obtained showed significant superiority of modified beta-binomial method. The effect of unbalancedness on the estimates of heritability and its precision has also been examined.

Key words: Stayability, Heritability, Beta-binomial, Unbalancedness.

1. Introduction

A number of economically important traits in dairy cattle breeding are recorded in all-or-none fashion. Examples of such traits are calving ease, retention to fixed age in the herd i.e. stayability and susceptibility to diseases etc. In literature a large number of methods are reported for the estimation of heritability of stayability. Recently Magnussen and Kremer [6] suggested the beta-binomial method for estimation of heritability of binary traits. In this, they suggested procedures of estimation of the parameters of the beta distribution by considering the weighting factor which adjusts for the proportionality between family mean probabilities and their variances. In the present study, this method is modified following the theoretical concepts given by Johnson and Kotz [5] for estimating parameter of beta distribution under the concept of equating the observed moments with that of their expected values in terms of parameter and further in turn, estimation of heritability of stayability. An attempt has also been made to study the comparative performance of this procedure with other different methods involving unbalanced data.

2 Material and Methods

Simulation Model

Before the concepts of different procedures are discussed, the data structure for the stayability is as under

In a given population the process is explained by a standardized Gaussion variable (Z) with mean zero and variance one. Whenever Z exceeds a certain threshold value, say Z' which is known, an outwardly observation character (δ) is expressed. This character is dichotomous on a binary scale, the character has a value of 1 for presence and 0 for absence.

The linear model for the observable variable Z is

$$Z_{iik} = \mu + S_i + e_{iik} \tag{1}$$

where Z_{iik} is the observation on the k^{th} individual in i^{th} family of j^{th} herd

μ is overall mean

S_i is ith family effect

eijk is the residual effect which consists of plot, herd and error effects

$$S_i \sim N(0, \sigma_f^2)$$
 and $e_{iik} \sim N(0, \sigma_e^2)$

Transformation of the intrinsic variable Z to a binary trait (δ) on the outward scale is done as follows

$$\begin{split} \delta_{ijk} &= 1 \text{ for } Z_{ijk} \leq Z' \text{ or } \Phi \left(Z_{ijk} \right) \leq P \\ &= 0 \text{ for } Z_{ijk} > Z' \text{ or } \Phi \left(Z_{ijk} \right) > P \end{split}$$

where Φ denotes the cumulative probability function of a normal distribution and P denote the population probability of observing the dichotomous character (δ).

2.1 Estimation of Heritability on Raw Data

The data with the half sib model is generated by the following model

$$Z_{ijk} = \mu + S_i + e_{ijk}$$

The true heritability or heritability on raw data is heritability which is computed using the original half sib simulated data Z_{ijk} without changing to a binary data.

The individual narrow sense heritability from the above model is

$$\hat{h}_{(Z)}^{2} = \frac{4\hat{\sigma}_{f}^{2}(z)}{\hat{\sigma}_{f}^{2}(z) + \hat{\sigma}_{e}^{2}(z)}$$
(2)

The estimated components are derived from an analysis of variance (Henderson's Method III, Searle et al. [7]) applied to the above model.

True family mean heritability is

$$\hat{h}_{f(Z)}^{2} = \frac{\hat{\sigma}_{f}^{2}(z)}{\hat{\sigma}_{f}^{2}(z) + \hat{\sigma}_{e}^{2}(z)/n_{herd} \times n_{offspring}}$$
(3)

For binary trait Dempster and Lerner [2] also gave the estimate of individual narrow sense heritability designated by h^2_{DL} which Gianola [4] further showed to be a special case of the more general solution as

$$\hat{\mathbf{h}}_{DL}^2 = 4\hat{\sigma}_f^2(\delta) \times [\phi(Z')]^{-2} \tag{4}$$

Where ϕ denotes the Gaussion probability density function evaluated at the threshold Z' for expression at the binary scale [Z' = ϕ^{-1} (P)] and $\sigma_f^{-2}(\delta)$ is the estimate of the family variance component obtained from analysis of variance (ANOVA) method applied to binary trait.

2.2 Heritability Estimation by Modified Beta-binomial Model Approach

In the case of stayability, the response is denoted by success and failure which follows the binomial distribution. These successes and failures can also be analysed for the estimation of heritability with the details as under

Let x_{ij} denote number of successes among the n_{ij} observations in the j^{th} subgroup in the i^{th} treatment group, where $1 \le j \le m_i$ and $1 \le i \le t$.

Assume

$$P_{r}(x_{ij} = x) = {n_{ij} \choose x} p_{ij}^{x} (1 - p_{ij})^{n_{ij} - x}, \quad 0 \le x \le n_{ij}$$
 (5)

where pij is a random variable from beta distribution with density function

$$\frac{p_i^{\alpha_i - 1}(1 - p_i)^{\beta_i - 1}}{B(\alpha_i, \beta_i)} \quad 0 < p_i < 1, \quad \alpha_i > 0, \quad \beta_i > 0$$
 (6)

The marginal distribution of xii, is then beta-binomial with

$$P_{r}(x_{ij} = x) = \frac{\binom{n_{ij}}{x} B(\alpha_{i} + x, n_{ij} + \beta_{i} - x)}{B(\alpha_{i}, \beta_{i})}$$
(7)

Following Magnussen and Kremer [6], three sets of beta parameters: one for phenotypic family probabilities, one for the family probabilities and one for the additive genetic probabilities are assumed for obtaining beta binomial based heritability estimates based on the model of δ_{iik} a binary trait data following

$$P_{iik} = p + p_i + p_{iik} \tag{8}$$

where P_{ijk} is the probability of observing the binary trait (δ) on the k^{th} individual in the j^{th} herd of family i, p is the overall population probability (fixed effect) and the remaining p's are the random contribution due to the family effect and residual effects respectively. From this model the three [Phenotypic (pf), family (f) and additive genetic (a)] variance components $\sigma_{pf}^{\ 2}(\delta)$, $\sigma_{f}^{\ 2}(\delta)$ and $\sigma_{a}^{\ 2}(\delta)$ can be obtained via a one-way analysis of variance performed on the binary data (δ_{iik}).

Phenotypic family probabilities $[p_{(pf)i}]$ are assumed to follow a beta distribution

$$p_{(pf)_i} = \sum_{jk} \frac{P_{ijk}}{n_{i..}} \text{ with } p_{(pf)_i} \sim \text{Beta} (\alpha_{pf}, \beta_{pf})$$
(9)

where $n_{i..}$ is the number of observations in the family i. Likewise family probabilities $[p_{(f)_i}]$ are defined as the sum of the overall mean (p) and an additive family effect.

$$p_{(f)_i} = p + p_i \text{ with } p_{(f)_i} \sim \text{Beta}(\alpha_f, \beta_f)$$
 (10)

Assuming that the families consist of half sibs the following conceptual model is used for the additive genetic family probabilities $[p_{(a)}]$.

$$p_{(a)} = p + 0.5p_i \text{ with } p_{(a)} \sim \text{Beta } (\alpha_a, \beta_a), \alpha_a, \beta_a > 0$$
 (11)

Sample estimates of the above probabilities are obtained from the data as

$$\hat{p}_{(pf)_{i}} = \sum_{ik} \frac{\delta_{ijk}}{n_{i}..} = \hat{p}_{(f)_{i}}$$
(12)

$$\bar{p} = \sum_{i} \frac{\hat{p}_{(pf)_i}}{n_{fam}} \tag{13}$$

Following Johnson and Kotz [5], estimates of the three sets of parameters can be obtained in the following way

The family of beta distribution is composed of all distribution with probability density functions of form

$$P_{y(Y)} = \frac{1}{B(\alpha, \beta)} \frac{(Y - a)^{\alpha - 1} (b - y)^{\beta - 1}}{(b - a)^{\alpha + \beta - 1}} \quad (a \le y \le b), \alpha, \beta > 0$$
 (14)

Estimation of all four parameters can be obtained by equating sample and population values of the first four moments.

If the values of a and b are known then only the first and second moments are given as

$$\mu_1' = \frac{a + (b - a)\alpha}{\alpha + \beta} \tag{15}$$

$$\mu_2 = (b-a)^2 \alpha \beta (\alpha + \beta)^{-2} (\alpha + \beta + 1)^{-1}$$
 (16)

where

$$\frac{\mu_1' - a}{b - a} = \frac{\alpha}{\alpha + \beta} \text{ and } \frac{\mu_2}{(b - a)^2} = \frac{\alpha}{\alpha + \beta} \left(1 - \frac{\alpha}{\alpha + \beta} \right) \frac{1}{\alpha + \beta + 1}$$
 (17)

Thus

$$\alpha + \beta = \frac{\mu_1' - a}{b - a} \frac{\left(1 - \frac{\mu_1' - a}{b - a}\right)}{\left(\frac{\mu_2}{(b - a)^2}\right)} - 1$$
 (18)

$$\alpha = \left(\frac{\mu_1' - a}{b - a}\right)^2 \left(1 - \frac{\mu_1' - a}{b - a}\right) \left(\frac{\mu_2}{(b - a)^2}\right)^{-1} - \frac{\mu_1' - a}{b - a}$$
(19)

Taking a = 0 and b = 1 the above equations reduced to

$$\alpha = \mu_1^2, \frac{(1 - \mu_1')}{\mu_2} - \mu_1' \tag{20}$$

$$\alpha + \beta = \mu_1 \cdot \frac{(1 - \mu_1')}{\mu_2} - 1 \tag{21}$$

Now, solving (15) and (16) and putting the value $\mu_1' = \overline{P}$ and $\mu_2 = \sigma_t^2$

Three sets of estimates can be written in a general way

$$\hat{\alpha}_{t} = \overline{P}^{2} \times \frac{(1 - \overline{P})}{\hat{\sigma}_{t}^{2}(\delta)} - \overline{P}$$
 (22)

$$\hat{\beta}_{t} = \frac{(1 - \overline{P})}{\overline{P}} \hat{\alpha}_{t} \tag{23}$$

Where the subscript t denotes the type of parameter [t = f (family), pf (phenotypic family mean), or a (additive genetic)] and $\hat{\sigma}_t^2(\delta)$ is the corresponding variance component estimated from the analysis of variance of the simulated binary trait (δ) .

Following Searle et al. [7] the conditional mean family probability in the selected population is expected to be

$$\bar{p}_{t/\delta} = \frac{\delta + \hat{\alpha}_t}{1 + \hat{\alpha}_t + \hat{\beta}_t} \tag{24}$$

where t = (f, pf, a) denotes the effect under consideration. The shift in mean due to this selection i.e. $(p_{t/\delta} - p)$ is considered to be a response to selection from which the expected realized heritability of the trait under selection can be estimated.

The estimate of selection response is

$$\Phi^{-1}(\mathbf{p}_{t/\delta}) - \Phi^{-1}(\mathbf{\bar{p}}) \tag{25}$$

Now the beta-binomial estimate of the "realized" individual narrow sense heritability is computed as

 h^2 = Expected response to selection/phenotypic selection differential (Falconer [3])

$$\hat{h}_{(beta)}^{2} = \frac{\left[\Phi^{-1}(p_{a/\delta}) - \Phi^{-1}(\overline{p})\right]}{\hat{i}}$$
 (26)

The beta distribution parameters can be used to compute the family mean heritability by taking the ratio of the additive family variance to that of phenotypic family variance.

$$h_{f(beta)}^{2} = \frac{\hat{\alpha}_{f} \times \hat{\beta}_{f} \times \left(\hat{\alpha}_{pf} + \hat{\beta}_{pf}\right)^{2} \times \left(\hat{\alpha}_{pf} + \hat{\beta}_{pf} + 1\right)}{\hat{\alpha}_{pf} \times \hat{\beta}_{pf} \times \left(\hat{\alpha}_{f} + \hat{\beta}_{f}\right)^{2} \times \left(\hat{\alpha}_{f} + \hat{\beta}_{f} + 1\right)}$$
(27)

The variance of a beta distribution with parameter a and b is

$$\frac{ab}{(a+b+1)(a+b)^2}$$

An alternative formula of the family mean heritability rooted in the beta-binomial model can be derived from the expected ratio of the "realized" selection response in family mean probability $(\overline{p}_{f/\delta} - \overline{p})$ to the selection response at the phenotypic family mean level $\frac{2 b (k-1)}{p-1}$. Transforming this ratio of responses to the scale of the intrinsic variable Z via the inverse to its cumulative distribution function yield an estimate of the realized family mean heritability.

$$h_{f(\Delta P/beta)}^{2} = \frac{\Phi^{-1}(\bar{p}_{f/\delta} = 1) - \Phi^{-1}(\bar{p})}{\Phi^{-1}(\bar{p}_{pf/\delta} = 1) - \Phi^{-1}(\bar{p})}$$
(28)

Further the comparison of different methods can be done on the basis of some measure of its precision. As all the estimates are not unbiased so the estimate of variance may not give a clear picture. In order to account the magnitude of the bias as well as some measure of precision, a measure called relative root mean square error is defined as

RMSE% =
$$\frac{\left[E(\text{estimate} - \text{true value})^2\right]^{0.5}}{\text{true value}} \times 100$$
 (29)

The degree of unbalancedness can be defined as

$$\Delta = N(n - \lambda)$$
 where $n = N/S$, $\sum_{i=1}^{s} n_i = N$

$$\lambda = \frac{1}{S - 1} \left[\sum_{i} n_{i} - \frac{\sum_{i} n_{i}^{2}}{N} \right]$$
 (30)

Here S = number of sires

 $n_i = number of daughters of ith sire$

N = total number of daughters

3. Results and Discussion

In order to compare the methods of estimation of heritability of stayability, different data sets with varying degree of unbalancedness have been simulated on computer for different parameters of heritability. The family structures are given in the following table.

S.No	No. of sire	Family of sire	Degree of unbalancedness	
1	5	10,10,10,10,10	0	
2	5	5,15,10,13,17	22.0	
3	5	3,4,13,11,19	44.00	
4	5	4,14,2,20,10	54.00	

Table 1. Different family structures

Table 2. Average estimates of individual narrow-sense heritability (h^2) and family mean heritability (h^2) of stayability for different degree of unbalanced data

Parameter		$h_s^2 = .2$		$h_s^2 = .25$		$h_s^2 = .3$	
Procedure	degree of unbalanced- ness	n _{herd} = 5	n _{herd} = 10	n _{herd} = 5	n _{herd} = 10	n _{herd} = 5	n _{herd} = 10
h _{rea(b)}	0	.1842	.2316	.2232	.2732	.2696	.3185
(U)		(.2360)	(.211)	(.2599)	(.2358)	(.2899)	(.2767)
	22.0	.1950	.2123	.2191	.2541	.2618	.2967
		(.2702)	(.1848)	(.2333)	(.2145)	(.2601)	(.1979)
	44.0	.1414	.2262	.2153	.2692	.2582	.3183
		(.3621)	(.2092)	(.2594)	(.2411)	(.2339)	(.2767)
	54.0	.1955	.2402	.2370	.2791	.2740	.3232
		(.2355)	(.2422)	(.3143)	(.2597)	(.3309)	(.2941)
h _f (beta)	0	.1196	.5437	.2063	.5940	.3368	.6665
n ₁ (ocus)		(.5660)	(.4792)	(.5489)	(.4796)	(.4916)	(.4786)
	22.0	.1950	.6003	.3080	.6577	.3996	.6993
		(.5246)	(.4597)	(.4679)	(.4113)	(.7746)	(.3793)
	44.0	.1414	.4742	.2312	.5588	.3017	.6223
		(.6520)	(.6390)	(.6634)	(.6480)	(.6313)	(.5509)
	54.0	.1955	.5205	.1509	.5768	.2231	.6102
		(.6021)	(.5026)	(.7332)	(.6684)	(.7291)	(.6189)
$h_f^2 \left(\frac{\Delta p}{\text{beta}} \right)$	0	.1259	.5471	.2174	.5976	.3414	.6658
		(.5981)	(.4894)	(.5588)	(.5135)	(.9257)	(.5320)
. /	22.0	.1943	.6040	.2314	.6617	.4024	.7036
		(.4740)	(.4635)	(.4844)	(.4156)	(.6454)	(.3820)
	44.0	.1437	.4780	.2313	.5633	.3035	.6273
		(.5906)	(.5709)	(.7876)	(.6447)	(.9332)	(.5570)
	54.0	.1578	.5259	.2489	.5811	.2214	.6142
	-	(.5723)	(.5655)	(.7253)	(.6742)	(.6329)	(.6295)

Parameter		$h_s^2 = .2$		$h_s^2 = .25$		$h_s^2 = .3$	
Procedure	degree of unbalanced- ness	n _{herd} = 5	$n_{\text{herd}} = 10$	n _{herd} = 5	$n_{\text{herd}} = 10$	n _{herd} = 5	n _{herd} = 10
h _{DL}	0	.2088	.2589	.2578	.3078	.3080	.3569
"DL		(.2710)	(.2585)	(.3096)	(.2953)	(.3595)	(.3342)
	22.0	.1972	.2356	.2510	.2815	.2998	.3917
		(.2484)	(.2232)	(.2808)	(.2627)	(.3197)	(.3019)
	44.0	.1322	.2475	.2408	.2956	.2888	.3463
		(.2565)	(.2437)	(.2338)	(.2224)	(.3317)	(.3227)
	54.0	.2181	.2654	.2701	.3166	.3240	.3672
		(.2934)	(.2777)	(.3227)	(.3211)	(.3332)	(.3297)
h _Z ²	0	.1918	.2134	.2376	.2577	.2829	.3017
"Z		(.1802)	(.1652)	(.2069)	(.1901)	(.2321)	(.2149)
	22.0	.1915	.2006	.2374	.2452	.2822	.2894
		(.1745)	(.1529)	(.2022)	(.1788)	(.2288)	(.2038)
	44.0	.1791	.2157	.2237	.2499	.2678	.3037
		(.1808)	(.1790)	(.2087)	(.2066)	(.2353)	(.2330)
	54.0	.1978	.2184	.2445	.2639	.2905	.3087
		(.2059)	(.1899)	(.2370)	(.2207)	(.2683)	(.2500)
$h_{f(z)}^2$	0	.3482	.7040	.4376	.7493	.5286	.7850
		(.6508)	(.6090)	(.6396)	(.5623)	(.4976)	(.4738)
	22.0	.4887	.7113	.5812	.7707	.6463	.8111
		(.7624)	(.5997)	(.5534)	(.3763)	(.4366)	(.2695)
	44.0	.3399	.7039	.4377	.7826	.5190	.7872
		(.4263)	(.3830)	(.3065)	(.2977)	(.7050)	(.2466)
	54.0	.3274	.6208	.3834	.6985	.4368	.7469
		(.7644)	(.6726)	(.5751)	(.5134)	(.5304)	(.3828)

In parentheses are the average standard deviations.

Data on Z_{ijk} are generated according to the linear model.

 $Z_{ijk} = \mu + S_i + e_{ijk}$ in series of half sib in the herd with size 5 and 10.

Family values (S_i) are simulated as a normal variate with mean zero and variance of 0.05, 0.0625 and 0.0811. Errors i.e. environmental values (e_{ijk}) are simulated as a single Gaussion variable with mean zero and variance 1. Five points of truncation or threshold levels (P) are used to convert normal data to binary data. The thresholds used are P = 0.05, 0.10, 0.15, 0.20, 0.25 which are the probabilities of observing the binary trait. Data are generated using different

parameters of heritability of stayability ($h_S^2 = 0.20, 0.25, 0.30$). For these parametric values, the samples are generated for 5 sires with different combination of daughters for each sire and is given in Table 1.

Table 3. Relative root mean square error (RMSE %) of selected estimates of heritability of stayability

Estimates		h _s ²	= .2	h _s ²	= .25	h _s ²	$h_s^2 = .3$	
Procedure	degree of unb- alanced -ness	n _{herd} =5	n _{herd} =10	n _{herd} =5	n _{herd} =10	n _{herd} =5	n _{herd} =10	
h _{rea(b)}	0	118.8051	107.0203	104.9426	95.1069	98.1486	92.9562	
iea(U)	22.0	103.5327	92,7798	94.3004	86.0768	88.3620	81.4460	
	44.0	115.3412	105.4735	105.3509	96.9910	99.5403	92.6944	
	54.0	136.1030	114.9707	114.7772	104.9387	111.5403	98.9781	
h _f ² (beta)	0	784.8375	486.5007	572.1008	329.3666	304.3085	162.6656	
	22.0	625.3346	308.8002	390.1128	234.4851	262.2488	186.6013	
	44.0	532.7427	510.8499	386.9533	323.0941	306.2420	213.8794	
	54.0	840.1959	394.4872	529.6447	261.5363	431.4547	300.2112	
$h_f^2 \left(\frac{\Delta p}{\text{beta}} \right)$	0	800.8952	491.9468	547.6036	435.2180	309.6845	217.6739	
	22.0	639.1647	295.4833	398.7281	228.9804	267.6749	187.8269	
	44.0	547.0746	566.0419	396.6207	326.6781	312.9305	215.2889	
	54.0	865.4541	399.4281	544.1143	304.5136	444.4058	304.0433	
h _{DL}	0	135.6594	132.5809	123.9184	120.3583	115.9497	113.0410	
"DL	22.0	138.2772	113.0403	112.3700	105.9000	110.2292	100.9548	
	44.0	140.3473	124.6503	117.5891	114.4408	110.6482	108.6652	
	54.0	150.1218	142.6503	137.9533	132.9313	131.3314	125.3138	
h _Z ²	0	90.2132	82.8892	82.9431	76.1128	77.7134	71.3376	
L	22.0	87.3433	76.4636	81.0307	71.5360	76.4676	68.0306	
	44.0	91.0101	89.8424	84.1309	82.7395	79.1743	77.6703	
	54.0	102.9975	95.4061	95.2009	88.4407	89.4848	83.3980	
$h_{f(z)}^2$	0	757.9289	395.4400	563.6870	300.7420	360.6789	226.0012	
1(2)	22.0	407.6288	335.3514	257.9600	256.9794	185.7674	172.6106	
	44.0	616.5689	316.7428	632.6874	233.6462	310.3746	182.0008	
	54.0	585.6509	486.3855	592.4560	272.6700	512.1513	196.0120	

The simulated data thus generated were subjected to different estimation procedures of heritability of stayability and results thus obtained are presented in Table 2. In case of true data points the estimates are less biased. But in case of family mean, heritability for true data points have more bias than family mean beta-binomial heritability estimates. It is also noticed from Table 2 narrow sense beta-binomial realized heritability (h²_{rea(b)}) is nearer to the parametric value. Dempster-Lerner estimates are the second closest to parametric value. But family mean heritability estimates are highly biased. One interesting point to note is that due to unbalancedness the standard errors are considerably high. Size of herd has great effect on the estimates as well on standard deviation.

For empirical comparison of different methods, the average root mean square error has found to be very handy tool and is calculated for different parametric values of heritability and over different threshold probabilities. The relative root mean square errors averaged over truncation probability for 5 sires with different number of daughters ranging from herd size 5 and 10 are shown in Table 3. From Table 3 it is clearly seen that the relative root mean square errors for family mean heritability estimates are significantly higher than any other heritability estimates. In case of herd size 10 the relative root mean square is less. The relative root mean square of the estimate of heritability for true data points shows the lowest value followed by beta binomial realized estimates.

From these results it is finally concluded that if one has an access to the assigned data of stayability than estimation of heritability based on this assigned data will yield very efficient and precise estimates and if one has only binary data of stayability then modified beta binomial estimates proved to be very accurate and precise in comparison to other methods of estimation. The unbalancedness however may sometimes lead to estimates with large standard errors and inconsistency.

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