

Performance evaluation of bootstrap strategies on the estimate of standard error of heritability by half-sib method

N OKENDRO SINGH¹, S D WAHI² and AMRIT KUMAR PAUL³

Directorate of Coldwater Fisheries Research, Bhimtal, Nainital 263 136 Uttarakhand

Received: 12 January 2009; Accepted: 15 July 2009

Key words: Bootstrap strategies, Heritability, Half-sib, Master sample

The important genetic parameter, heritability indicates the relative importance of the genetic and environmental sources of variation in the character and is termed as degree of genetic determination of the character. Singh and Wahi (2003) obtained the optimum family size and structure for estimating the standard error of heritability in half-sib model. Singh *et al.* (2006) studied the robustness of bootstrap estimates of variance of heritability to master samples by drawing independent master samples in half-sib model. Keeping in view the importance of bootstrap technique the performance of different bootstrap strategies on estimate of the precision of heritability in half-sib model is investigated in depth.

Simulation of sample data

The linear model for the measurement of Y_{ij} , on the progeny of the j th dam ($j=1, 2, \dots, d$) mated to the i th sire ($i=1, 2, \dots, s$) can be written as:

$$Y_{ij} = \mu + s_i + e_{ij},$$

where μ is the general mean, s_i the effect of i th sire and e_{ij} the error deviation. Let us assume that all the effects are random and independent with expectations:

$$E(s_i) = E(e_{ij}) = 0,$$

and variances

$$E(S_i^2) = \sigma_s^2,$$

$$E(e_{ij}^2) = \sigma_e^2.$$

We follow Ronningen's (1974) approach to simulate half-sib data by:

$$Y_{ij} = \mu + \sigma_s S_i + \sigma_e e_{ij},$$

where S_j and e_{ij} are random standard normal variables. From the simulated data the heritability can be estimated as:

$$\hat{h}^2 = \frac{4\hat{\sigma}_s^2}{\hat{\sigma}_s^2 + \hat{\sigma}_e^2}$$

Generation of Bootstrap samples: Following bootstrap method by Aastveit (1990) bootstrapping was done by 3 different approaches, viz. at sire level as well as at progeny level (strategy I), at sire level alone (strategy II) and at progeny level alone (strategy III). The algorithm of bootstrapping is explained here.

The data set generated was considered as the master sample. The sires were then numbered sequentially. Using random number generator integers with the maximum of the total number of sires were generated. According to the random numbers, sires were selected and within the selected sire, progenies were again chosen randomly as done for sire selection (strategy I). In case of strategy II, sires were randomly selected as done above with all the progenies falling in the selected sire. Strategy III consists of selecting all the sires, but within the selected sires progenies were chosen at random in the similar fashion. This constitutes our first bootstrap sample or bootstrap replicate. Thus, using the next random number, the second bootstrap replicate was selected and this process was continued until the required number of bootstrap replications was obtained.

Analysis of samples

From the original sample generated according to half-sib model, the estimates of heritability were obtained by the usual formula. Then for the sample data using the traditional methods, variances (standard errors) of the estimates were calculated. In the case of sib analysis, if 't' happens to be the intra-class correlation coefficient estimate, the variance of 't' given by Fisher (1950) is

$$\hat{\sigma}_t^2 = \frac{2\{1+(n-1)t\}^2}{n(n-1)(N-1)}(1-t)^2$$

where 'n' is the number of offsprings per sib class, and 'N' is the number of such classes. The variance of heritability estimator half-sibs in given by:

$$\hat{\sigma}_h^2 = 16 \hat{\sigma}_t^2$$

Present address: ¹Scientist (Senior Scale) ²Principal Scientist, ³Senior Scientist.

Table 1. Bootstrap estimates of mean, bias, percentage bias, standard error and asymptotic standard error of different heritability values for optimum family structures by half-sib method

Sample size	Structure (s, p)*	Heritability														
		Master sample					Bootstrap									
Est.	S.E.	Rep (%)	¹ Est.	¹ Bias	¹ SE	¹ Asymp SE	² Est.	² Bias (%)	² SE	² Asymp SE	³ Est.	³ Bias (%)	³ SE	³ Asymp SE		
Heritability=0.1																
80	(2, 40)	0.326	0.361	100	0.195	-0.131 (40)	0.326	0.476	0.125	-0.201 (62)	0.215	0.420	0.376	0.050 (15)	0.342	0.589
		0.298	0.345	200	0.198	-0.100 (34)	0.325	0.478	0.081	-0.217 (73)	0.200	0.379	0.316	0.018 (06)	0.330	0.555
		0.282	0.336	400	0.173	-0.109 (39)	0.321	0.459	0.109	-0.173 (61)	0.191	0.406	0.346	0.064 (23)	0.330	0.573
		0.249	0.316	800	0.171	-0.078 (31)	0.317	0.458	0.081	-0.168 (67)	0.176	0.379	0.318	0.069 (28)	0.330	0.557
200	(5, 40)	0.194	0.176	100	0.253	0.059 (30)	0.187	0.258	0.098	-0.080 (41)	0.103	0.213	0.298	0.104 (54)	0.182	0.272
		0.155	0.157	200	0.206	0.051 (33)	0.171	0.242	0.104	-0.046 (30)	0.098	0.197	0.240	0.085 (55)	0.162	0.254
		0.148	0.154	400	0.189	0.041 (28)	0.167	0.236	0.071	-0.048 (32)	0.094	0.201	0.241	0.093 (63)	0.162	0.254
		0.142	0.151	800	0.187	0.045 (32)	0.159	0.235	0.070	-0.053 (37)	0.080	0.197	0.245	0.103 (73)	0.162	0.255
400	(10, 40)	0.096	0.088	100	0.191	0.095 (99)	0.140	0.158	0.084	-0.012 (13)	0.075	0.127	0.191	0.095 (99)	0.117	0.158
		0.108	0.093	200	0.171	0.063 (58)	0.127	0.153	0.089	-0.019 (18)	0.075	0.129	0.210	0.102 (94)	0.098	0.162
		0.110	0.094	400	0.191	0.081 (74)	0.124	0.158	0.084	-0.026 (24)	0.071	0.127	0.214	0.104 (95)	0.095	0.163
		0.099	0.089	800	0.183	0.084 (85)	0.111	0.156	0.083	-0.016 (16)	0.066	0.127	0.196	0.097 (98)	0.091	0.159
800	(20, 40)	0.106	0.065	100	0.194	0.088 (83)	0.094	0.109	0.087	-0.019 (18)	0.061	0.088	0.205	0.099 (93)	0.075	0.111
		0.112	0.067	200	0.194	0.082 (73)	0.092	0.109	0.099	-0.013 (12)	0.061	0.091	0.208	0.096 (86)	0.067	0.111
		0.102	0.064	400	0.180	0.078 (76)	0.086	0.107	0.091	-0.011 (11)	0.055	0.089	0.202	0.100 (98)	0.066	0.110
		0.112	0.067	800	0.199	0.087 (78)	0.085	0.110	0.103	-0.009 (08)	0.055	0.092	0.204	0.092 (82)	0.065	0.111

Heritability=0.25																
80	(5, 16)	0.297	0.345	100	0.480	0.183 (62)	0.440	0.573	0.220	-0.077 (26)	0.286	0.480	0.498	0.201 (68)	0.378	0.579
		0.278	0.334	200	0.417	0.139 (50)	0.440	0.553	0.220	-0.058 (21)	0.278	0.480	0.494	0.216 (78)	0.359	0.577
		0.436	0.418	400	0.504	0.068 (16)	0.432	0.580	0.276	-0.160 (37)	0.272	0.503	0.594	0.158 (36)	0.359	0.605
		0.316	0.355	800	0.450	0.134 (42)	0.400	0.564	0.222	-0.094 (30)	0.271	0.480	0.547	0.231 (73)	0.324	0.593
200	(10, 20)	0.269	0.207	100	0.380	0.111 (41)	0.239	0.308	0.213	-0.056 (21)	0.159	0.267	0.453	0.184 (68)	0.205	0.323
		0.263	0.205	200	0.400	0.137 (52)	0.236	0.313	0.213	-0.050 (19)	0.159	0.267	0.451	0.188 (71)	0.200	0.323
		0.250	0.200	400	0.390	0.140 (56)	0.233	0.310	0.208	-0.042 (17)	0.152	0.266	0.437	0.187 (75)	0.199	0.320
		0.282	0.213	800	0.340	0.058 (21)	0.232	0.299	0.223	-0.059 (21)	0.142	0.270	0.451	0.169 (60)	0.197	0.323
400	(25, 16)	0.266	0.146	100	0.480	0.214 (80)	0.193	0.220	0.221	-0.045 (17)	0.150	0.196	0.527	0.261 (98)	0.145	0.240
		0.231	0.136	200	0.450	0.219 (95)	0.175	0.216	0.220	-0.011 (05)	0.126	0.196	0.482	0.251 (108)	0.141	0.234
		0.248	0.141	400	0.479	0.231 (93)	0.170	0.220	0.233	-0.015 (06)	0.111	0.198	0.480	0.232 (94)	0.134	0.234
		0.261	0.144	800	0.466	0.205 (79)	0.161	0.218	0.240	-0.021 (08)	0.102	0.199	0.489	0.228 (87)	0.133	0.235
800	(50, 16)	0.260	0.102	100	0.484	0.224 (86)	0.150	0.164	0.243	-0.017 (07)	0.107	0.140	0.491	0.231 (89)	0.100	0.165
		0.300	0.110	200	0.527	0.227 (76)	0.132	0.168	0.287	-0.013 (04)	0.090	0.145	0.519	0.219 (73)	0.098	0.167
		0.231	0.096	400	0.453	0.222 (96)	0.123	0.161	0.231	0.000 (00)	0.081	0.138	0.470	0.239 (103)	0.097	0.163
		0.245	0.099	800	0.475	0.230 (94)	0.122	0.163	0.242	-0.003 (01)	0.081	0.140	0.480	0.235 (96)	0.096	0.164
80	(8, 10)	0.564	0.475	100	0.863	0.299 (53)	0.480	0.685	0.468	-0.096 (17)	0.350	0.607	0.860	0.296 (52)	0.365	0.684
		0.535	0.463	200	0.774	0.239 (45)	0.443	0.670	0.426	-0.109 (20)	0.345	0.596	0.872	0.337 (63)	0.353	0.686
		0.566	0.476	400	0.774	0.208 (37)	0.433	0.670	0.456	-0.110 (19)	0.332	0.604	0.856	0.290 (51)	0.352	0.684

(Contd...)

(Table 1. Concluded)

Sample size	Structure (s, p)*	Heritability														
		Master sample						Bootstrap								
		Est.	S.E.	Rep (%)	¹ Est.	¹ Bias	¹ SE	¹ Asymp SE	² Est.	² Bias (%)	² SE	² Asymp SE	³ Est.	³ Bias (%)	³ SE	³ Asymp SE
200	(20, 10)	0.540	0.465	800	0.798	0.258 (48)	0.420	0.674	0.470	-0.070 (13)	0.324	0.607	0.847	0.307 (57)	0.341	0.682
		0.481	0.277	100	0.799	0.318 (66)	0.319	0.409	0.460	-0.021 (04)	0.246	0.367	0.833	0.352 (73)	0.240	0.413
		0.490	0.280	200	0.799	0.309 (63)	0.310	0.409	0.458	-0.032 (07)	0.228	0.367	0.845	0.355 (72)	0.232	0.414
400	(40, 10)	0.531	0.291	400	0.823	0.292 (55)	0.301	0.412	0.478	-0.053 (10)	0.219	0.370	0.875	0.344 (65)	0.227	0.417
		0.536	0.293	800	0.812	0.276 (51)	0.298	0.411	0.489	-0.047 (09)	0.210	0.371	0.729	0.193 (36)	0.222	0.402
		0.487	0.197	100	0.818	0.331 (68)	0.228	0.287	0.472	-0.015 (03)	0.173	0.258	0.811	0.324 (67)	0.175	0.287
800	(80, 10)	0.479	0.196	200	0.818	0.339 (71)	0.216	0.287	0.450	-0.029 (06)	0.170	0.255	0.830	0.351 (73)	0.152	0.288
		0.507	0.201	400	0.821	0.314 (62)	0.205	0.287	0.472	-0.035 (07)	0.162	0.258	0.862	0.355 (70)	0.152	0.290
		0.468	0.193	800	0.801	0.333 (71)	0.204	0.286	0.447	-0.021 (04)	0.156	0.255	0.818	0.350 (75)	0.152	0.287
		0.509	0.143	100	0.866	0.357 (70)	0.171	0.204	0.510	0.001 (00)	0.139	0.184	0.855	0.346 (68)	0.117	0.203
		0.520	0.144	200	0.863	0.343 (66)	0.166	0.204	0.512	-0.008 (02)	0.127	0.184	0.876	0.356 (68)	0.112	0.204
		0.495	0.141	400	0.846	0.351 (71)	0.157	0.203	0.492	-0.003 (01)	0.123	0.182	0.841	0.346 (70)	0.111	0.203
		800	0.876	0.335 (62)	0.151	0.204	0.524	-0.017 (03)	0.116	0.185	0.878	0.337 (62)	0.110	0.204		

* (s,p): stands for the number of sires and p, for the number of progenies per sire. ¹ Bootstrapping is done both at the sire and progeny levels. ² Bootstrapping at the sire level only. ³ Bootstrapping at the progeny level only.

Abbreviations: Est, Estimate; SE, standard error; Rep, replication; Asymp, asymptotic.

By making use of these estimators, the standard errors of the sample estimators were obtained.

Singh *et al.* (2006) reported under the strategy I that the optimum family size for low, moderate and high heritability are about 40, 16–20 and 10 respectively. The present investigation deals with comparison of three different bootstrap strategies for optimum family size with respect to bootstrap estimates of heritability, bias, standard error and asymptotic estimates of standard error presented in Table 1. The asymptotic estimate standard error of heritability is always higher than the corresponding bootstrap estimate for all the 3 strategies. There is considerable reduction in standard error for all the values of heritability with increase in sample size from 80–800 and with increase in number of bootstrap replications within the given family size and structure. The strategy II gave lower estimates of standard error as compared to strategy I irrespective of sample size and structure. Also, the estimate of standard error by strategy II is always lower than the strategy III except when the number of sires is extremely larger than the number of progenies per sire for a given sample size. In rest of the cases the performance of strategies I and III are approximately equivalent. The corresponding difference among the estimates of standard error by different strategies reduces considerably with increase in sample size irrespective of the heritability values. The bias in the bootstrap estimates of heritability are quite high in strategy I and III and it varies from 16–99% and 6–108% of the estimates respectively. The bias does not reduce even with increase in sample size in both the cases. On the contrary the bias in bootstrap estimates of heritability in strategy II are comparatively lower and reduce from 62–8% for low heritability, 37–1% for moderate and from 20–1% in case of high heritability with increase in heritability value as well as with increase in sample size. Although strategy III unusually showed superior or nearly equivalent performance as compared to others when the number of sire is larger than the number of progeny per sire, we conclude that the strategy II of bootstrapping at sire level alone has shown the best performance to other strategies considered for estimating the precision of heritability as well as for the parameter estimation.

SUMMARY

The bootstrap estimates of standard error of heritability using half-sib model were obtained by drawing independent master samples for optimum family size by 3 different bootstrap strategies. In strategy I, the bootstrapping was done both at sire level as well as at progeny level whereas in strategy II and III, it was done only at the sire level and progeny level, respectively. The strategy II performed better than the other 2 bootstrap strategies for estimating the parameter - heritability and its precision. The bias in the estimates of heritability in strategy II is also found to be minimum as compared to the other two strategies.

REFERENCES

- Aastveit A H. 1990. Use of bootstrapping for estimation of standard deviation and confidence intervals of genetic variance and covariance component. *Biometrical Journal* **32**: 515–27.
- Fisher R A. 1950. *Statistical Methods of Research Workers*. 11th edn. Oliver Boyd, Edinburgh.
- Ronningen K. 1974. Monte-Carlo simulation of statistical biological models, which are of interest in animal breeding. *Acta Agriculture Scandinavica* **24**: 135–42.
- Singh N, Okendro and Wahi S D. 2003. Effect of sample size and structure on the bootstrap estimate of variance of heritability. *Indian Journal of Animal Sciences* **73** (5): 545–48.
- Singh N Okendro, Rao A R, Wahi S D and Singh V P. 2006. Robustness of bootstrap estimates of variance of heritability to master samples in half-sib analysis. *Indian Journal of Animal General Breeding*. **27** (1–2): 6–11.