Estimation of Heritability Using Some Auxiliary Traits in Dairy Cattle

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SUMMARY

Retention of cow is an important character in dairy cattle which needs a thorough genetic analysis. Herdlife, which is influenced by production as well as other auxiliary characters, is another viewpoint of retention. It is seen that related characters, have a sizable effect on retention. Because of this reason, a complete theoretical expression which takes into account of these relationships for estimation of heritability of retention (herdlife), has been worked out. To validate the proposed theory, simulation has been used. It is seen that, adjustment or correction, which depends upon various parameters such as heritability, phenotypic correlation, genetic correlation etc., has a sizable effect on estimates of heritability of herdlife. Further relative absolute bias has also been studied and it is found that reduction in relative absolute bias is significant due to adjustment of herdlife for related auxiliary traits.

Key words : Herdlife, Auxiliary traits, Heritability, Relative absolute bias.
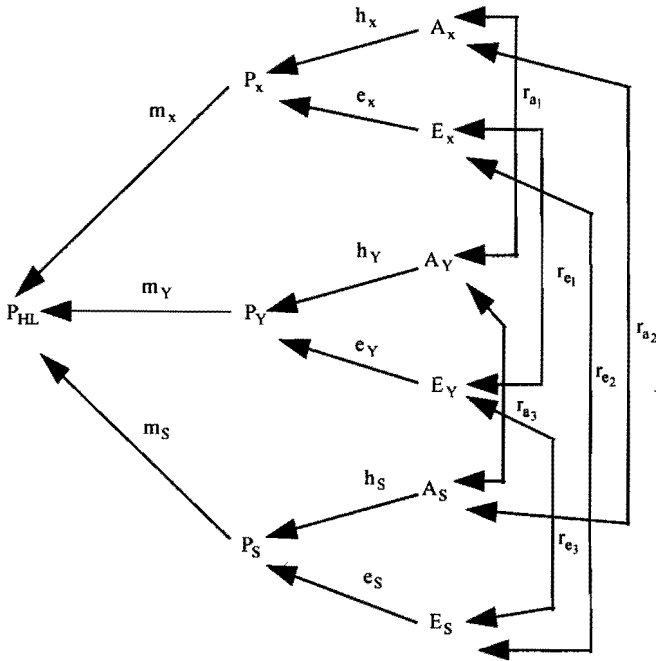
1. Introduction

In dairy cattle breeding, stayability or herdlife is an important economic character. Stayability, an aptitude to stay in the herd, is determined by culling decisions of individual producers. Stayability can also be defined as the capability for an animal to remain productive in the herd over time. Most culling decisions are economic in nature, a cow is replaced because higher profit is expected from her replacement. Herdlife is influenced by culling decisions which in turn are determined by various production and non-production traits. Non-production traits include reproductive performance, health management, type traits and workability traits etc.

In past studies, on one hand it has been shown that there exists positive phenotypic and genetic correlations between production and herdlife but on the other hand strong past selection for production has not resulted in a related response in herdlife. This apparent contradiction was explained by Van Arendonk [5]. He argued that strategies for improvement of herdlife should be

directed for increasing the ability of cows to survive regardless of production. Many field studies have further shown that adjustments for cow's phenotypic production will yield a true picture of herdlife termed as 'functional herdlife' and is thought to be related more closely to·survival. In order to include this character in breeding program, the genetics of this character is very important. With this background, in the present study, an attempt has been made to obtain an estimate of heritability of this complex character i.e. herdlife or stayability or survival adjusted for characters which are themselves related.

2. Estimation of Heritability

For dairy cows, length of productive life, or herdlife is a trait of major economic importance and is influenced by many traits. Out of many traits, some characters are intercorrelated and some are not. Diagramatically the influence of two correlated characters can be visualized as

Fig. 1. Path diagram : Relationship among udder depth (X), production (Y), stayability (S) and herdlife (HL); P_I, A_I and E_I, are phenotype, breeding value and environment respectively for trait $I (= X, Y, S, HL)$. Path coefficient h_I, e_I and m_I $(I = X, Y, S)$ respresent square root of heritability, $\sqrt{(1 - h^2)}$ and standardized partial regression coefficient of P_{HL} on P_I respectively. r_a and r_e are genetic and environmental correlations respectively.
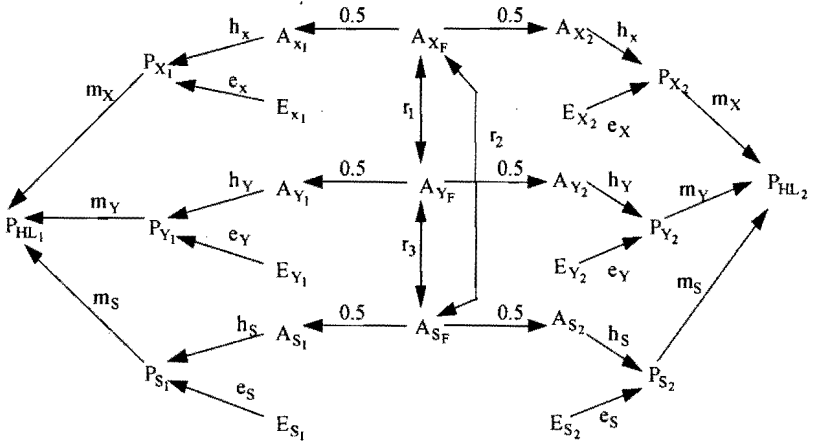
Fig. 2. Path diagram : Relationship among production, udder depth, stayability and herdlife of two half-sib offspring (1,2) of sire A.

Based on the theory of path coefficients and following Dekkers [1], besides production, herdlife taken as a measure of survival, is influenced by additional character say udder depth. The estimate of heritability can be obtained from the usual correlation between two half sibs.

$$\hat{h}^2_{HL} = 4r(P_{HL_1}, P_{HL_2})$$
$$= m_X^2 h_X^2 + m_Y^2 h_Y^2 + m_S^2 h_S^2 + 2 m_X m_S h_X h_S r_2$$
$$+ 2 m_X m_Y h_X h_Y r_1 + 2 m_Y m_S h_Y h_S r_3 \qquad (1)$$

If herdlife consist of only two characters i.e. production and survival, then this is reduced to

$$\hat{h}^2_{HL} = m_Y^2 h_Y^2 + m_S^2 h_S^2 + 2m_Y m_S h_Y h_S r_a$$

This can easily be generalized for the number of characters as

$$\hat{h}^2_{HL} = \sum_i m_i^2 h_i^2 + \sum_i \sum_{\substack{j \\ i \neq j}} m_i m_j h_i h_j r_{g(i, j)}, \quad (i, j = 1, 2, ..., n) \qquad (2)$$

2.1 Analysis for Herdlife Adjusted for Production and Udder Depth

Herdlife adjusted for production (HL/Y) can be obtained by regression procedure

$$P_{HL/Y} = P_{HL} - r_{Y,HL} \, P_Y \qquad \text{where } [r_{Y, HL} = m_Y + m_S \, r_P]$$
$$= m_S (P_S - r_P P_Y)$$

It can be extended to two characters by assuming a cow's phenotypic value of herdlife (P_{HL}) to be a linear function of production (P_Y), survival (P_S) and udder depth (P_X).

$$P_{HL} = m_X \, P_X + m_Y \, P_Y + m_S \, P_S \tag{3}$$

Here survivability include all factors affecting herdlife except production and udder depth. Variables considered here are assumed to be standardized normal.

From the path diagram (1) we can write

$$r_{P_1} = r \, (P_X, P_Y) = h_X \, r_{a_1} \, h_Y + e_X \, r_{e_1} \, e_Y \tag{4}$$

$$r_{P_2} = r \, (P_X, P_S) = h_X \, r_{a_2} \, h_S + e_X \, r_{e_2} \, e_S \tag{5}$$

$$r_{P_3} = r \, (P_Y, P_S) = h_Y \, r_{a_3} \, h_S + e_Y \, r_{e_3} \, e_S \tag{6}$$

Here, $e_i = \sqrt{1 - h_i^2}$ \hfill (7)

$$r_{X, HL} = m_X + m_Y \, r_{P_1} + m_S \, r_{P_2} \tag{8}$$

$$r_{Y, HL} = m_Y + m_X \, r_{P_1} + m_S \, r_{P_3} \tag{9}$$

$$V(P_{HL}) = m_X{}^2 + m_Y{}^2 + m_S{}^2 + 2 \, m_X \, m_Y \, r_{P_1}$$
$$+ \, 2 \, m_Y \, m_S \, r_{P_3} + 2 m_X \, m_S \, r_{P_2} = 1 \tag{10}$$

If adjustment is done for the character production (Y) and other trait (X), we can write

$$P_{HL/Y,X} = P_{HL} - r_{Y, HL} \, P_Y - r_{X,HL} \, P_X$$
$$= m_S \, (P_S - r_{P_2} \, P_X - r_{P_3} \, P_Y) - r_{P_1} \, (P_Y \, m_X + P_X \, m_Y) \tag{11}$$

$$V(P_{HL/Y, X}) = 1 - r^2{}_{Y,HL} - r^2{}_{X,HL} + 2 \, r_{X,HL} \, r_{Y,HL} \, r_{P_1} \tag{12}$$

The estimate of heritability of herdlife adjusted for production is

$$\hat{h}^2_{HL/Y} = 4r(P_{HL_1/Y_1}, P_{HL_2/Y_2})$$
$$= \frac{h_S^2 - 2r_P r_a h_Y h_S + r_P^2 h_Y^2}{1 - r_P^2}$$

whereas the estimate of heritability of herdlife adjusted for production and udder depth is

$$\hat{h}^2_{HL/Y, X} = 4r(P_{HL_1/Y_1, X_1}, P_{HL_2/Y_2, X_2}) = 4A/B$$

where

$$A = \frac{1}{4} \, m_S^2 \, (h_S^2 - 2r_2 r_{P_2} \, h_X h_S - 2r_3 r_{P_3} h_S + 2r_{P_2} r_{P_3} r_1 h_X h_Y + r_{P_2}^2 \, h_X^2 + r_{P_3} \, h_Y^2)$$

$$+ \frac{1}{4} m_S m_X (2r_{P_1} r_{P_3} \, h_Y^2 - 2r_{P_1} r_3 h_Y h_S + 2r_{P_1} r_{P_2} r_1 h_X h_Y)$$

$$+ \frac{1}{4} m_S m_Y \left(2 r_{P_1} r_{P_2} h_X^2 - 2 r_{P_1} r_2 h_X h_S + 2 r_{P_1} r_{P_3} r_1 h_Y h_X \right)$$

$$+ \frac{1}{4} r_{P_1}^2 \left(m_X^2 h_Y^2 + 2 r_1 m_X m_Y h_X h_Y + m_Y^2 h_X^2 \right) \tag{13}$$

$$B = m_S^2 (1 - r_{P_2}^2 - r_{P_3}^2 + 2 r_{P_1} r_{P_2} r_{P_3}) + r_{P_1}^2 (m_X^2 + m_Y^2 + 2 r_{P_1} m_X m_Y$$

$$+ 2 r_{P_2} m_S m_X + 2 r_{P_3} m_S m_Y) \tag{14}$$

If we generalize it for more than two characters, then we can write

$$A = \frac{1}{4} m_S^2 \left[h_S^2 - 2 \sum_{i=1}^{n} r_g(S, i) r_P(S, i) h_S h_i + \sum r_P^2(S, i) h_i^2 \right.$$

$$\left. + \sum_i \sum_{\substack{j \\ i \neq j}} r_P(S, i) r_P(S, j) h_i h_j \right]$$

$$+ \frac{1}{4} m_S \sum_{i=1}^{n} 2 m_i \left[\sum_{j=1}^{n} \left(r_P(S, j) r_P(i, j) h_j^2 - r_P(i, j) r_g(S, j) h_S h_j \right. \right.$$

$$\left. \left. + r_P(i, j) r_P(S, i) r_g(i, j) h_i h_j \right) \right]$$

$$+ \frac{1}{4} \sum_i^{n} \sum_{\substack{j \\ i \neq j}}^{n} r_P^2(i, j) \left[(m_i h_j + m_j h_i)^2 - 2(1 - r_g(i, j)) m_i m_j h_i h_j \right] \tag{15}$$

$$B = m_S^2 \left[1 - \sum_{i=1}^{n} r_P^2(S, i) + \sum_i^{n} \sum_{\substack{j \\ i \neq j}}^{n} r_P(i, j) r_P(S, i) r_P(S, j) \right]$$

$$+ \sum_{i=1}^{n} \sum_{\substack{j=1 \\ i \neq j}}^{n} r_P^2(i, j) \left(m_i^2 + 2 m_S r_P(S, i) m_i + 2 r_P(i, j) m_i m_j \right) \tag{16}$$

3. Validation of Developed Theory

In order to study the applicability and efficiency of the developed procedure the empirical comparison is done on simulated data. Simulation is used to test the derived formula. The data on half sib is generated by assuming the usual half sib model as

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

where

Y_{ij} is the record of jth offspring of the ith sire

μ is general mean

s_i is ith sire effect, $s_i \sim N(0, \delta_S^2)$

e_{ij} is error effect, $e_{ij} \sim N(0, \delta_e^2)$

Following Ronningen [3] the first character, udder depth, is generated using simple half sib model

$$PX(i, j) = \mu_X + b_X \delta_X + e_X \delta_{eX}$$

where b_X and e_X are standard normal variates. The second character i.e. production (Y) is generated by retaining the relationship of X and Y as

$$PY(i, j) = \mu_X + r_I \delta_{SY} b_X + \sqrt{1 - r_I^2}\, \delta_{SY} b_Y + r_{el}\, \delta_{eY} e_X + \sqrt{1 - r_{el}^2}\delta_{eY} e_Y$$

where r_I and r_{el} are genetic and environmental correlation between Y and X.

The third character, stayability (Z), is generated in the same way retaining the relationship between X and Y, X and Z, and Y and Z. Results of the proposed method are illustrated on simulated data. The usefulness and application of developed theory has also been illustrated on real data.

4. One Character Influencing Herdlife

For this, parametric values i.e. $h_Y^2 = 0.25$ (heritability of production), $r_a = -0.2$ (genetic correlation of production and stayability), $r_{Y,HL} = 0.25$ (Phenotypic correlation between production and herdlife), $m_Y = 0.4$ (Standardized partial regression coefficient of herdlife on production) which were reported by Dekker [1] and Essl [2], are used. Four different values of heritability of stayability i.e. $h_S^2 = 0.05, 0.10, 0.15$ and 0.20 are used. Data thus generated are subjected to path analysis approach. Results are given in Table 1 and Table 2.

Table 1. Comparison of estimates of heritabilities of herdlife as a measure of survival based on simulation and theoretical derived expression for h_S^2

Input parameters are h_Y^2 (heritability of production) = 0.25, r_a (genetic correlation between production and survival) = –0.2, phenotypic correlation between production and herdlife = 0.25 and m_Y (standardized partial regression coefficient of herdlife on production) = 0.4

| | $h_S^2 = 0.05$ | | | | $h_S^2 = 0.10$ | | | |
| | Simulation | | Theoretical | | Simulation | | Theoretical | |
	Estimate	RAB%	Estimate	RAB%	Estimate	RAB%	Estimate	RAB%
Herdlife	0.0818	63.6	0.0705	41.0	0.1232	23.2	0.1112	11.2
	(.0318)		(.0205)		(.0232)		(.0112)	
Herdlife adjusted for production	0.0617	23.4	0.0502	0.4	0.1108	10.8	0.0985	1.5
	(.0117)		(.0002)		(.0108)		(-.0015)	

Figures in the brackets indicate bias of the estimate.

From this table it is seen from the results that there is a close association between the results obtained from simulation and that obtained by derived formula. This clearly validates the theory developed here. In case of $h_S^2 = 0.05$, the estimate of heritability of herdlife without adjustment is 0.0818, whereas for herdlife adjusted for production, it is reduced to 0.0617. As the character, survival, is related to fitness so even such a small change is also of great significance and clearly implies that true heritability of survival in the form of adjusted herdlife for production plays an important evolutionary role.

Table 2. Comparison of estimates of heritabilities of herdlife as a measure of survivability based on simulation and theoretical derived expression for h_S^2

Input parameters are h_Y^2 (heritability of production) = 0.25, r_a (genetic correlation between production and survival) = – 0.2, phenotypic correlation between production and herdlife = 0.25 and m_Y (standardized partial regression coefficient of herdlife on production) = 0.4

| | $h_S^2 = 0.15$ | | | | $h_S^2 = 0.20$ | | | |
| | Simulation | | Theoretical | | Simulation | | Theoretical | |
	Estimate	RAB%	Estimate	RAB%	Estimate	RAB%	Estimate	RAB%
Herdlife	0.1592	6.1	0.1569	4.6	0.2153	7.6	0.1970	1.5
	(.0092)		(.0069)		(.0153)		(-.003)	
Herdlife ajusted for production	0.1545	3.0	0.1475	1.6	0.1953	2.3	0.1978	1.1
	(.0045)		(-.0025)		(-.0119)		(-.0022)	

Figures in the brackets indicate bias of the estimate.

The same trend is noticed in case of the heritability $h_S^2 = 0.10$, 0.15 and 0.20. Due to non availability of explicit expression for the second degree statistics, the standard deviations are not presented for the estimates of heritability. However, for comparison purpose, the percent relative absolute bias from the true value is calculated using the formula

$$RAB = \frac{|\text{estimate} - \text{true value}|}{\text{true value}} \times 100$$

From the results, it is noted that the values of RAB for the estimate of heritability of herdlife for $h_S^2 = 0.05$ are 63.6 and 23.4 for without adjustment and with adjustment, respectively. The corresponding values are 23.2 and 10.8 for the $h_S^2 = 0.10$. On further examining it is seen that the relative reduction in RAB due to adjustment for the value of $h_S^2 = 0.05$ is around 63%, whereas it is 53% in case of $h_S^2 = 0.10$. This implies that adjustment is very important in reducing the bias and thus helps and leads to more accurate and precise estimate of heritability.

5. Consideration of Two Characters

For this situation two characters i.e. production and udder depth are considered. Parametric values are taken from Short *et al.* [4] and Dekker [1]. Data are simulated on the basis of some prior knowledge about the parametric values of h_X^2 (heritability of udder depth character) = 0.26, h_Y^2 (heritability of production) = 0.25, $r_{X,HL}$ (Phenotypic correlation of herdlife and udder depth) = 0.15, $r_{Y,HL}$ (Phenotypic correlation between herdlife and production) = 0.25, r_1 (Genetic correlation between production and udder depth) = –0.4, r_2 (Genetic correlation between udder depth and stayability) = 0.2, r_3 (Genetic correlation between production and stayability) = – 0.2, r_{P_1} (Phenotypic correlation between production and udder depth) = –0.3, r_{P_2} (Phenotypic correlation between udder depth and stayability) = 0.08, r_{P_3} (Phenotypic correlation between production and stayability) = –0.1029, m_Y (Standardized regression coefficient of herdlife on production) = 0.4, m_X (Standardized regression coefficient of herdlife on udder depth) = 0.2. Four heritabilities of stayability $h_S^2 = 0.05$, 0.10, 0.15 and 0.20 are used. Simulated data are further analyzed and the results are tabulated in Table 3 and Table 4.

Table 3. Estimates of heritability of herdlife and herdlife adjusted
for production and udder depth

	$h_S^2 = 0.05$				$h_S^2 = 0.10$			
	Simulation		Theoretical		Simulation		Theoretical	
	Estimate	RAB%	Estimate	RAB%	Estimate	RAB%	Estimate	RAB%
Herdlife	0.0749	49.8	0.0647	29.4	0.1146	14.6	0.0998	0.2
	(0.0249)		(0.0147)		(0.0146)		(-0.0002)	
Herdlife adjusted for production and udder depth	0.0486	2.8	0.0506	1.2	0.0963	3.7	0.0999	0.1
	(-0.0014)		(0.0006)		(-0.0037)		(-0.0001)	

Figures in the brackets indicate bias of the estimate.

It is seen that both for $h_S^2 = 0.05$ and $h_S^2 = 0.1$, the adjustment done is overcorrection for the estimate of heritability in case of simulated data sets and have lower values than the true parametric value which means that the value of bias is of negative sign. The reason for overcorrection could be that both the characters, production and udder depth, are themselves related and may cause more correction than is desired. However, the results from derived expression are very well in accordance with the theory. Bias in heritability estimates in the case of derived formula are smaller than that of simulated estimates. Bias in the estimate of heritability of herdlife which is not adjusted is 0.0249 but for adjusted, it is -0.0014 for the case of $h_S^2 = 0.05$.

Table 4. Estimates of heritability of herdlife and herdlife adjusted
for production and udder depth

	$h_S^2 = 0.15$				$h_S^2 = 0.20$			
	Simulation		Theoretical		Simulation		Theoretical	
	Estimate	RAB%	Estimate	RAB%	Estimate	RAB%	Estimate	RAB%
Herdlife	0.1652	10.1	0.1622	8.1	0.2115	5.7	0.2012	6.0
	(0.0152)		(0.0122)		(0.0115)		(0.0012)	
Herdlife adjusted for production and udder depth	0.1595	6.3	0.1586	5.7	0.2029	1.4	0.2005	0.2
	(0.0095)		(0.0086)		(0.0029)		(0.0005)	

Figures in the brackets indicate bias of the estimate.

Further it is also noticed that higher the heritability the lesser is the bias i.e. the bias are much lower for $h_S^2 = 0.10$ in comparison to $h_S^2 = 0.05$. Estimate of heritability of herdlife adjusted for production is 0.0617 and it is 0.0486 in case

of adjustment for two characters i.e. production and udder depth, whereas the true heritability is $h_S^2 = 0.05$. From Table 3, it is noticed that the RAB for the estimates of heritability of herdlife for $h_S^2 = 0.05$ are 49.8 and 2.8 for without and with adjustment, respectively. The corresponding values for $h_S^2 = 0.10$ are 14.6 and 3.7. Here reduction in RAB is 94% in case of $h_S^2 = 0.05$ and 74% in case of $h_S^2 = 0.10$. This implies that for two related characters adjustment is even more intense and effective than one character.

6. Illustration on Real Data

Data collected from the history sheets of Military Dairy Farms, Ambala, under the project "Measurement of genetic improvement due to scientific breeding in cattle and buffaloes", have been utilised for illustration. The characters from the records of history sheets are total life time production (TLTP) as herdlife, first lactation yield (FLY) as production, age at disposal (AD) as non-production character. Age at first calving (AFC) and number of lactations (NL) correlated with production, have also been extracted. The data consists of 10 sires with total number of 151 daughters, using the technique of half-sib analysis of variance, the estimate of heritability of stayability has been obtained as $h_S^2 = 0.527$.

Table 5. Estimates of heritability of herdlife along with bias and RAB

True estimate of $h_S^2 = 0.527$			
Estimate of heritability of herdlife as obtained from	Estimate	Bias	RAB (%)
(a) Herdlife without adjusted for production	0.1670	-0.36	68.31
(b) Herdlife adjusted for production	0.2765	-0.250	47.53
(c) Herdlife without adjusted for production and age at disposal	0.1640	-0.363	68.88
(d) Herdlife adjusted for production and age at disposal	0.5220	-0.005	0.95
(e) Herdlife without adjusted for production and number of lactations	0.1600	-0.367	69.64
(f) Herdlife adjusted for production and number of lactations	0.6200	0.093	17.65

From Table 5, it is seen that estimates of heritability of herdlife, as obtained from herdlife without adjustment for production, production and age, production and number of lactations are as 0.1670, 0.1640 and 0.1600 respectively. If one adjusts for production alone it becomes 0.2765 and 0.5220 if one adjusts for production and age at disposal, and finally rises to 0.6200 if one adjusts for production and number of lactations. It is clear from these results that production and age at disposal are two important constituents of survival in a

herd as the value of heritability obtained on adjustment by these characters is very close to the true estimate of heritability of herdlife of 0.527. The over correction in the case of number of lactations is probably due to vague/rough idea of number of lactations while recording, because even an incomplete, or few days of calving, is considered as a full lactation whereas, ideally, only 305 days of lactation should only be considered as complete lactation. Because of this very reason number of lactations has been considered to give a rough idea about the survival in the herd.

Finally, it is concluded that heritability is a very important genetic parameter and has to be estimated with extra care. The aim of getting the true estimate of heritability can thus only be achieved by extracting all the information affecting this complex character. Thus if prior information on the relationship between herdlife and production and other reproductive traits are available, then it is desired that this may be included for calculating the true estimate of heritability obtained from path coefficient approach. Even small adjustment in the estimate of heritability of herdlife which is related to fitness, plays a significant role in formulating further breeding strategies for genetic improvement and thus must be considered to study its inheritance.

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