# A Revisit to Satterthwaite Approximation to the Distribution of a Linear Combination of Sample Mean Squares 

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#### Abstract

SUMMARY Linear combinations of mean squares occur in many areas of research like statistical hypothesis testing, design of experiments, and statistical genetics. The present paper demonstrates how the Satterthwaite approximation dating back to early nineteenth century is still a potential tool to reduce complicated problems to a solvable format. Significantly, a new derivation of the distribution of a linear combination of 'Between sires' and 'Between dams within sires' mean squares under certain restrictions is proposed which is quite simple compared the Graybill (1956) approach to the problem.


Keywords: Linear combination of mean squares, Satherthwaite approximation.

## 1. INTRODUCTION

Satterthwaite approximation as it was originally proposed in 1946 by F.E. Satterthwaite is a method to find the approximate distribution of a linear combination of independent estimates of variance-components. This becomes handy in all situations where the problem at hand boils down to finding the distribution of a linear combination of mean squares. It is used in adopting a valid test for equality of main plot treatment means of a Split-plot experimental design. It has its application in computing the probability of inadmissible estimates of heritability from different mating designs for animal experiments. In testing the equality of means of two samples from normal populations, it is applied to get a pooled estimate of variance based on the two samples. The purpose of this paper is to discuss the Satterthwaite procedure and delineate the procedure in specific situations.

## 2. THE SATTERTHWAITE (1946) APPROXIMATION

Let $\sigma_{1}^{2}, \sigma_{2}^{2,}, \ldots, \sigma_{k}^{2,}$ be the basic variances pertaining to a variance component analysis with $s_{1}^{2}, s_{2}^{2,}, \ldots, s_{k}^{2}$ as their estimates respectively. Further let

$$
V=\sum_{i=1}^{k} \omega_{i} \sigma_{i}^{2}
$$

and

$$
v=\sum_{i=1}^{k} \omega_{i} s_{i}^{2}
$$

Clearly $v$ is an unbiased estimate of $V$. When both $v$ and $V$ are essentially positive, the probability density of $v$ can be approximated to

$$
\begin{equation*}
\frac{\chi^{2}}{f} \cdot V \tag{2.1}
\end{equation*}
$$

where $\chi^{2}$ is distributed as Chi-square with degrees of freedom,

$$
f=I \sum_{i=1}^{k} \omega_{i} \sigma_{i}^{2} I^{2} \div \sum_{i=1}^{k} \omega_{i}^{2} \sigma_{i}^{4} f_{i}^{-1}
$$

in which $f_{i}$ is the degrees of freedom corresponding to $s_{i}^{2}$.

It must be noted that $s_{i}^{2}(i=1,2, \ldots, k)$ are the $k$ mean squares and $\sigma_{i}^{2}(i=1,2, \ldots, k)$ their expectations, such that $E(v)=V$.

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## 3. USE OF THE APPROXIMATION IN PROBLEM AREAS

### 3.1 Testing equality of main plot treatment effects in split plot design

The structure of ANOVA for split plot experiments is as given in Table 3.1. The existence of the term $r \sigma_{t v}^{2}$ in the expectation of $T$ is arising from defining $t_{j}^{\prime} s$ as averages over the whole population of varieties. Due to this the variance ratio T/W cannot be used to test the significance of split plot treatments. Cochran and Cox (1950) suggested that the ratio $(T+S) /$ ( $W+I$ ) could be used as the criterion. Alternately, Kempthorne (1967) proposed the ratio, $(T / W+I-S)$ . The theoretical justification for the use of these two ratios is given below.

Table 3.1. Analysis of variance for Split-Plot experiments

| Source | $d . f$ | $\boldsymbol{M} . \boldsymbol{S}$ | $\boldsymbol{E} . \boldsymbol{M} . \boldsymbol{S}$ |
| :---: | :---: | :---: | :---: |
| Blocks | $(r-1)$ |  |  |
| Treatments <br> (T) | $(t-1)$ | $T$ | $\sigma_{s}^{2}+v \sigma_{w}^{2}+r \sigma_{t v}^{2}+\frac{r v}{t-1} \sum\left(t_{j-} \bar{t}\right)^{2}$ |
| Error <br> (whole plot) | $(r-1)(t-1)$ | $W$ | $\sigma_{s}^{2}+v \sigma_{w}^{2}$ |
| Varieties (S) | $(v-1)$ | $V$ | $\sigma_{s}^{2}+r \sigma_{t v}^{2}+r t \sigma_{v}^{2}$ |
| T $\chi$ S | $(t-1)(v-1)$ | $I$ | $\sigma_{s}^{2}+r \sigma_{t v}^{2}$ |
| Error <br> (split plot) | $(r-1) t(v-1)$ | $S$ | $\sigma_{s}^{2}$ |

From Table 3.1, we have

$$
\begin{aligned}
& E(T)=\sigma_{s}^{2}+v \sigma_{w}^{2}+r \sigma_{t v}^{2}+\frac{r v}{t-1} \sum\left(t_{j-\bar{t}}\right)^{2} \\
& E(W+I-S)=\sigma_{s}^{2}+v \sigma_{w}^{2}+r \sigma_{t v}^{2}
\end{aligned}
$$

Under the null hypothesis, $T$ is a $\frac{\chi^{2}}{(t-1)} \theta_{1}$, where $\theta_{1}=\sigma_{s}^{2}+v \sigma_{w}^{2}+r \sigma_{v v}^{2}$. Taking recourse to the Satterthwaite approximation, we find, $(W+I-S)$ has an approximate $\frac{\chi^{2}}{f_{2}} \cdot \theta_{1}$ distribution with $f_{2}$ degrees of
freedom freedom
where

$$
\begin{align*}
& f_{2}=I W+I-S J^{2} \cdot\left[\frac{W^{2}}{(r-1)(t-1)}+\frac{I^{2}}{(t-1)(v-1)}+\right. \\
& \frac{S^{2}}{(r-1) t(v-1)} I^{-1} \tag{3.1}
\end{align*}
$$

Note that in the expression for $f_{2}$, estimates $W, S$ and $I$ have been used in place of their expectations. Clearly, the ratio $T /(\mathrm{W}+\mathrm{I}-\mathrm{S})$ has approximate $F$ distribution with $(t-1)$ and $f_{2}$ degrees of freedom and can be used to test the hypothesis that $t_{j}$ 's are equal.

In a similar vein it can be shown that $T+S$ and $W+I$ are $\frac{\chi^{2}}{n_{1}} \theta_{2}$ and $\frac{\chi^{2}}{n_{2}} \theta_{2}$ respectively,
where

$$
\begin{align*}
& \theta_{2}=2 \sigma_{s}^{2}+v \sigma_{w}^{2}+r \sigma_{t v}^{2} \\
& n_{1}=(T+S)^{2} \cdot\left[\frac{T^{2}}{(t-1)}+\frac{S^{2}}{(r-1) t(v-1)} l^{-1}\right. \tag{3.2}
\end{align*}
$$

and

$$
\begin{equation*}
n_{2}=(W+I)^{2} \cdot\left[\frac{W^{2}}{(r-1)(t-1)}+\frac{I^{2}}{(t-1)(v-1)} I^{-1}\right. \tag{3.3}
\end{equation*}
$$

Accordingly, the ratio $(T+S) /(\mathrm{W}+\mathrm{I})$ can be compared with the tabled value of $F_{n_{1}, n_{2}}$ to find out significant differences in $t_{j}$ 's if any.

### 3.2 Test of equality of two sample means when variances are unequal

Consider two random samples of sizes $n_{1}$ and $n_{2}$ drawn from normal populations with means $\mu_{1}, \mu_{2}$ and unequal variances $\sigma_{1}^{2}$ and $\sigma_{2}^{2}$. Suppose we are interested in testing the null hypothesis $H_{0}: \mu_{1}=\mu_{2}$ based on the means $\bar{X}, \bar{Y}$, and mean squares $s_{1}^{2}$ and $s_{2}^{2}$ computed from the samples.

Using Satterthwaite approximation the statistic, $v=\left(s_{1}^{2} / n_{1}\right)+\left(s_{2}^{2} / n_{2}\right)$ has $\frac{\chi^{2}}{f} . V$ distribution where, $V=E(v)=\left(\sigma_{1}^{2} / n_{1}\right)+\left(\sigma_{2}^{2} / n_{2}\right)$ and $f$ is given by the expression

$$
\begin{equation*}
f=I\left(\left(\sigma_{1}^{2} / n_{1}\right)+\left(\sigma_{2}^{2} / n_{2}\right) J^{2} \cdot\left[\frac{1}{\left(n_{1}-1\right)}\left(\sigma_{1}^{2} / n_{1}\right)^{2}+\right.\right. \tag{3.4}
\end{equation*}
$$

$\frac{1}{\left(n_{2}-1\right)}\left(\sigma_{2}^{2} / n_{2}\right)^{2} J^{-1}$
which can be estimated by $\hat{f}$ which is obtained by replacing with $\sigma_{1}^{2}$ and $\sigma_{2}^{2}$ in Eq.(3.4) by their corresponding mean squares. Also, the unknown Vi s estimated by its estimate $v$. Then it immediately follows that $\bar{X}-\bar{Y}$ is $\sqrt{V} N(0,1)$ and so,

$$
t=(\bar{X}-\bar{Y}) / \sqrt{v}
$$

has approximate $t$ distribution with $\hat{f}$ degrees of freedom, where

$$
\begin{aligned}
& \quad \hat{f}=I\left(s_{1}^{2} / n_{1}\right)+\left(s_{2}^{2} / n_{2}\right) J^{2} \cdot\left[\frac{1}{\left(n_{1}-1\right)}\left(s_{1}^{2} / n_{1}\right)^{2}+\right. \\
& \frac{1}{\left(n_{2}-1\right)}\left(s_{2}^{2} / n_{2}\right)^{2} J^{-1}
\end{aligned}
$$

For large sample size, $t$ tends to $N(0,1)$ and the hypothesis can be tested by using normal probability tables.

Now consider an extension of this to the case involving $k$ independent normal populations, the ith sample coming from, $N\left(\mu_{i}, \sigma_{i}^{2}\right)$ with mean and mean squares as $\bar{Y}_{i}$ and $s_{i}^{2}$ respectively.

Let $M=\sum_{i} c_{i} \mu_{i}$ and $\hat{M}=\sum_{i} c_{i} \bar{Y}_{i}$ be its unbiased estimate. To test the hypothesis $\hat{M}=\mathrm{M}$, one can consider the test statistic

$$
\begin{equation*}
T=\frac{\hat{M}-\mathrm{M}}{\sqrt{\sum c_{i}^{2}}\left(\frac{s_{i}^{2}}{n_{i}}\right)} \tag{3.5}
\end{equation*}
$$

Under the null hypothesis $\hat{M}-M=0, T$ will have an approximate $t$ distribution with $v$ degrees of freedom where

$$
v=I \sum_{i} \frac{1}{n_{i}} c_{i}^{2} s_{i}^{2} J^{2} \cdot \sum_{i}\left\{\left(c_{i}^{2} s_{i}^{2} / n_{i}\right)^{2} /\left(n_{i}-1\right)\right\}^{-1}
$$

### 3.3 Obtaining the probability of inadmissible estimates of heritability

The first attempt in this direction is perhaps that of Gill and Jensen (1968) who derived the theoretical probabilities of negative estimates of $h^{2}$ from both half-sib and full-sib analyses, confining to the additive model of gene action. Prabhakaran and Jain (1987a,b,c, 1988, 1990), Prabhakaran and Sharma (1994, 1995), Prabhakaran and Seema Jaggi (1996) analyzed the problem in greater detail covering negative and positive inadmissible estimates from various mating designs under a more general model, i.e. the additive-dominance-epistasis model and worked out the sample size requirement for various situations. Jogendra Singh (1992) extended the study to cover heritability under practical definition while Shukla (1993) discussed heritability estimation under finite
population assumptions, its effect on the probability of inadmissible estimates and related saving in sample requirement. In the present paper, our illustration of the use of Satterthwaite approximation to obtain the probability of inadmissible estimates will be confined to the full-sib correlation heritability only. Form of analysis of variance based on the Full-sib model is given in Table 3.2.

Table 3.2. Analysis of variance for full-sib data

| Source | $d . f$ | M.S | E.M.S |
| :---: | :---: | :---: | :---: |
| Between sires | $(s-1)$ | $\boldsymbol{A}$ | $\sigma_{1}^{2}=\sigma_{w}^{2}+n \sigma_{d}^{2}+n d \sigma_{s}^{2}$ |
| Between dams/sires | $s(d-1)$ | $\boldsymbol{B}$ | $\sigma_{2}^{2}=\sigma_{w}^{2}+n \sigma_{d}^{2}$ |
| Between progeny/ | $s d(n-1)$ | $\boldsymbol{C}$ | $\sigma_{3}^{2}=\sigma_{w}^{2}$ |
| dams/sires |  |  |  |

The mean squares for the three classifications are distributed as follows:

$$
\begin{aligned}
& A \sim \chi_{(s-1)}^{2}\left\{\left(\sigma_{w}^{2}+n \sigma_{d}^{2}+n d \sigma_{s}^{2}\right) /(s-1)\right\} \\
& B \sim \chi_{s(d-1)}^{2}\left\{\left(\sigma_{w}^{2}+n \sigma_{d}^{2}\right) / s(d-1)\right\} \\
& C \sim \chi_{s d(n-1)}^{2}\left(\sigma_{w}^{2}\right) / s d(n-1)
\end{aligned}
$$

The estimate of the intra-class correlation between paternal half-sibs is given by

$$
t_{1}=\frac{A-B}{A+(d-1) B+d(n-1) C}
$$

and for maternal half-sibs, it is

$$
t_{2}=\frac{d(B-C)}{A+(d-1) B+d(n-1) C}
$$

Using $t_{1}$ and $t_{2}$, three estimates of heritability can be obtained:

$$
\begin{align*}
& h_{S}^{2}=4 t_{1} \\
& h_{D}^{2}=4 t_{2} \\
& h_{(S+D)}^{2}=2\left(t_{1}+t_{2}\right) \tag{3.6}
\end{align*}
$$

The estimates $h_{S}^{2}$ and $h_{D}^{2}$ are known as sire component and dam component heritability respectively, while $h_{(S+D)}^{2}$ is a combined estimate using both sire and dam components.

Now the expression for probability of negative estimates based on (sire+dam) components combined can be obtained as follows:

$$
\begin{align*}
& P\left(h_{S+D}^{2}<0\right)=P\left[S_{s}^{2}+S_{d}^{2}<0\right] \\
& =P[A+(d-1) B<d C\rceil \tag{3.7}
\end{align*}
$$

Using Satterthwaite (1946) approximation,
$A+(d-1) B \sim \frac{\chi_{1}^{2}}{a} V_{1}$
where

$$
a=\frac{\left[\sigma_{1}^{2}+(d-1) \sigma_{2}^{2}\right]^{2}}{\left\{(s-1)^{-1} \sigma_{1}^{4}+(d-1)^{2}[s(d-1)]^{-1} \sigma_{2}^{4}\right\}} \quad \text { is the }
$$

degrees of freedom of $\chi_{1}^{2}$

$$
\begin{align*}
& =\left[\frac{\left[1+(d-1) \eta_{1} J^{2} s(s-1)\right.}{s+(d-1)(s-1) \eta_{1}^{2}}\right]  \tag{3.9}\\
& V_{1}=\left[\sigma_{1}^{2}+(d-1) \sigma_{2}^{2}\right\rfloor=\frac{d \sigma_{P}^{2}}{2}\left[2+(n-1) h^{2}\right] \tag{3.10}
\end{align*}
$$

$\sigma_{P}^{2}=\sigma_{s}^{2}+\sigma_{d}^{2}+\sigma_{w}^{2}$ is the total observational variance
and

$$
\begin{equation*}
\eta_{1}=\frac{\sigma_{2}^{2}}{\sigma_{1}^{2}}=\frac{4+(n-2) h^{2}}{4+(n d+n-2) h^{2}} \text { and } C \sim \frac{\chi^{2}}{s d(n-1)} \sigma_{3}^{2} \tag{3.11}
\end{equation*}
$$

Therefore, using Equations (3.8) to (3.11) in Eq.(3.7) and noting that

$$
\begin{align*}
& \sigma_{3}^{2}=\frac{\sigma_{P}^{2}}{2}\left[2-h^{2}\right), \text { it follows that } \\
& P\left(h_{S+D}^{2}<0\right)=P\left[F_{a, s d(n-1)}<d \frac{\sigma_{3}^{2}}{V_{1}}\right] \\
& =P\left[F_{a, s(n-1)}<\frac{2-h^{2}}{2+(n-1) h^{2}}\right] \tag{3.12}
\end{align*}
$$

The probabilities can be computed for different combinations of $s, d$ and $h^{2}$ fixing $n$ at a desired level (say $=2$ ), using any computational algorithm for $F$ cumulative probabilities.

Prabhakaran and Jain (1987c) have observed that the computed probabilities of negative estimates based on Satterthwaite (1946) and Hastings (1955) approximations are in perfect agreement with the exact values computed using the distributional properties of $\alpha X-\beta Y$ where $X, Y$ independent $\chi^{2}$ variates and $\alpha, \beta$ positive constants. Therefore the probabilities from simulated data is least likely to yield any new information and hence not considered here. Hence, the
probability of negative estimates $h_{S+D}^{2}$ for combinations of $10,20,50$ and 100 sires and $6,10,20$ and 30 dams and for $h^{2}=0.10$ and $n=2$ obtained from the new procedure are presented in Table 3.3

This table shows that the Sire-Dam components (combined) estimate requires nearly 3000 observations from 50 sires to get a non-negative estimate in $97 \%$ of the cases, whereas sire-component estimate based on half this number would have given non-negative estimate in $99 \%$ of the cases. The Sire-Dam estimate based on 2000 observations is expected to be nonnegative in $94 \%$ of the cases. Also for increasing the chance of getting a non-negative estimate, it is more advantageous to use more observations per sire than attempting to evaluate more sires for a fixed total number of observations.

Table 3.3. Probability of negative estimates of heritability $\left(h_{S+D}^{2}\right)$ from full-sib analysis with two progeny per mating when $h^{2}$ of the trait is around 0.10

| Dams per sire |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: |
| Sires | 6 | 10 | 20 | 30 |
| 10 | $(\mathrm{~N}=120)$ | $(\mathrm{N}=200)$ | $(\mathrm{N}=400)$ | $(\mathrm{N}=600)$ |
|  | 36.7 | 32.1 | 24.9 | 20.3 |
| 20 | $(\mathrm{~N}=240)$ | $(\mathrm{N}=400)$ | $(\mathrm{N}=800)$ | $(\mathrm{N}=1200)$ |
|  | 31.2 | 25.4 | 16.8 | 11.8 |
| 50 | $(\mathrm{~N}=600)$ | $(\mathrm{N}=1000)$ | $(\mathrm{N}=2000)$ | $(\mathrm{N}=3000)$ |
|  | 21.6 | 14.6 | 6.3 | 3.0 |
| 100 | $(\mathrm{~N}=1200)$ | $(\mathrm{N}=2000)$ | $(\mathrm{N}=4000)$ | $(\mathrm{N}=6000)$ |
|  | 13.2 | 6.7 | 1.5 | 0.4 |

### 3.4 A simple and quick solution to a problem posed in Graybill et al. (1956)

The purpose of Graybill et al. (1956) was to present a method of confidence limits of heritability based on full-sib correlation. According to the authors the method presented was patterned after the procedure used by Satterthwaite (1941) for testing a hypothesis on variance components. The method proposed was essentially based on finding the approximate distribution of a linear combination of 'between sires' $(A)$ and 'between dams within sires' $(B)$ mean squares under certain conditions stipulated. To be more precise, he sought to obtain the approximate distribution of

$$
\begin{equation*}
\frac{Y}{N}=\frac{\alpha A+\beta B}{\sigma_{4}^{2}} \tag{3.13}
\end{equation*}
$$

such that $\sigma_{4}^{2}=\sigma_{w}^{2}+\gamma\left(\sigma_{s}^{2}+\sigma_{d}^{2}\right)$ so that $\left(\frac{Y}{N}\right)\left(\frac{C}{\operatorname{sd}(n-1)}\right)^{-1}$ will be approximately distributed as a Snedecor's $F_{N, s(n-1)}$ which was to be used to obtain the approximate confidence limits on $h_{S+D}^{2}$.

Instead of applying the Satterthwaite principle directly, the authors adopted a lengthy and involved derivation based on the moment generating function of ( $Y / N$ ).

A simpler solution to the problem is summarized below, using parameters defined in Table 3.2.

By Satterthwaite principle, $\alpha A+\beta B \sim \frac{\chi^{2}}{N} v$ where $\chi^{2}$ is a Chi-square with $N$ degrees of freedom and we have

$$
\begin{align*}
& \quad E(\alpha \mathrm{~A}+\beta \mathrm{B})=\alpha \sigma_{1}^{2}+\beta \sigma_{2}^{2}=\alpha\left[\sigma_{w}^{2}+n \sigma_{d}^{2}+n d \sigma_{s}^{2}\right]+ \\
& \beta\left[\sigma_{w}^{2}+n \sigma_{d}^{2}\right]  \tag{3.14}\\
& N=\frac{\left(\alpha \sigma_{1}^{2}+\beta \sigma_{2}^{2}\right)^{2}}{(s-1)^{-1}\left(\alpha \sigma_{1}^{2}\right)^{2}+[s(d-1)]^{-1}\left(\beta \sigma_{2}^{2}\right)^{2}} \tag{3.15}
\end{align*}
$$

and the restriction

$$
\begin{equation*}
\sigma_{4}^{2}=\sigma_{w}^{2}+\gamma\left(\sigma_{s}^{2}+\sigma_{d}^{2}\right) \tag{3.16}
\end{equation*}
$$

Equating the coefficients of $\sigma_{w}^{2}, \sigma_{s}^{2}$ and $\sigma_{d}^{2}$ at (3.14) and (3.16) we get,

$$
\alpha+\beta=1, \text { and } n(\alpha+\beta)=n d \alpha \text { or } \alpha+\beta=d \alpha
$$

Solving these equations, we find
$\alpha=(1 / d)$ and $\beta=(d-1) / d$ and hence $\gamma=n$

It may be observed that

$$
\begin{equation*}
\frac{\sigma_{1}^{4}}{\sigma_{4}^{4}}=\frac{\left[\sigma_{w}^{2}+n \sigma_{d}^{2}+n d \sigma_{s}^{2}\right]^{2}}{\left[\sigma_{w}^{2}+n\left(\sigma_{s}^{2}+\sigma_{d}^{2}\right)\right]^{2}}=I \frac{1+n d K}{1+n K} I^{2}, \tag{3.18}
\end{equation*}
$$

using $\sigma_{s}^{2} / \sigma_{w}^{2}+n \sigma_{d}^{2}=K$, and $\gamma=n$
Likewise,

$$
\begin{equation*}
\frac{\sigma_{2}^{4}}{\sigma_{4}^{4}}=I \frac{1}{1+n K} I^{2} \tag{3.19}
\end{equation*}
$$

Using (3.18) and (319) in Eq.(3.15) and setting $\alpha=(1 / d)$ and $\beta=(d-1) / d$ we get

$$
\begin{equation*}
N=\frac{s(s-1) d^{2}(1+n K)^{2}}{(s-1)(d-1)+s(1+n d K)^{2}} \tag{3.20}
\end{equation*}
$$

It immediately follows from (3.13) that
$\frac{Y}{N}=\frac{\alpha A+\beta B}{\sigma_{4}^{2}} \sim \frac{\chi^{2}}{N}$
and therefore, $\quad\left(\frac{Y}{N}\right)\left(\frac{C}{s d(n-1)}\right)^{-1}$ has an approximate $F_{N, s d(n-1)}$ density.

## 4. DISCUSSION AND CONCLUSION

The material of sections 3.3 and 3.4 are original theoretical developments by the author that have not been reported in any journals. The other two are just reviews on the topic, to abreast the inquisitive readers of the theoretical work that took place in the area. All these results stemmed from theoretical or practical problems, which needed further theoretical developments and considerations, for better understanding and clear solution. In conclusion, the author wish to instill in the young generation of workers, that the thrill of working with theoretical problems emerging from other known problems is far more enjoyable than those without this probing ingredient in their core. This is, perhaps the reason why we always enjoyed, and derived inspiration from, reading R.A. Fisher's theoretical works in the areas of Statistical-genetics, Design of experiments, or Derivation of theoretical distributions or any other. This is how one of Fishers last Ph.D. students, Walter Bodmer ${ }^{\#}$ described Fisher, in a personal review:
"The vast majority of his theoretical work was, as he himself often emphasized, devoted to an understanding of how to deal with real experimental data. He, for example, collected data in the field on the three forms of the primrose, Primula vulgaris, a subject that in the end formed a major part of my initial research in genetics under his guidance. Fisher remained throughout his life a keen observer of the natural world."

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