A COMPUTER PROGRAM FOR CALCULATION AND
STATISTICAL COMPARISON OF INTRINSIC RATES OF
INCREASE AND ASSOCIATED LIFE TABLE PARAMETERS

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ABSTRACT

An often crucial component in the study of insects is the determination of reproductive capabilities. While it is important to study reproduction at the level of the individual, it is often more desirable to develop a standardized estimate of the growth rate of insect populations. One such estimator, the intrinsic rate of increase ($r_m$), has been used for many years by insect ecologists. This statistic is useful not only as a measure of population growth potential but also as a bioclimatic index and a natural enemy rating parameter. Recently introduced methods to calculate variances for $r_m$ values have increased the utility of the statistic, enabling comparisons of growth rates from different species or biotypes. Although these values are usually calculated with the help of a computer, programs to perform the required computations have not been widely available. In this paper we describe a computer program, written in Pascal, designed to simplify the calculation of intrinsic rates of increase and associated Jackknife estimates of variance. The program also computes (1) approximate confidence intervals, (2) several commonly used fertility table parameters with their standard errors, and (3) daily means for some of these parameters, which can be used for graphing data.

RESUMEN

Un componente crucial que ocurre a menudo en el estudio de insectos es la determinación de la capacidad de reproducción. Mientras que es importante estudiar la reproducción al nivel del individuo, a menudo es más deseable desarrollar un estimado patrón de la tasa de crecimiento de las poblaciones de insectos. Un tal estimador, la tasa intrínseca de aumento ($r_m$), ha sido usado por ecologistas de insectos por muchos años. Esta estadística es útil no solo como una medida del potencial de crecimiento de la población, pero también como un índice bioclimático y un parámetro natural de la tasa del enemigo. Métodos introducidos recientemente para calcular la varianza de los valores $r_m$ han aumentado la utilidad de la estadística, lo que ha permitido comparar la tasa de crecimiento entre diferentes especies o biotipos. Aunque estos valores son calculados usualmente con la ayuda de una computadora, los programas para llevar a cabo las computaciones requeridas no han estado comúnmente disponibles. En este trabajo nosotros describimos un programa de computadora escrito en Pascal, diseñado para simplificar la calculación de tasas de aumentos intrínsecos y los estimados asociados de varianza Jackknife. El programa también computa (1) intervalos aproximados de confianza, (2) algunos parámetros comúnmente usados en tablas de fertilidad con su patrón de errores, y (3) promedio diario para algunos de esos parámetros, los cuales se pueden usar para hacer gráficos de los datos.

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An often crucial component in the study of insects is the determination of reproductive capacities. While it is important to study reproduction at the level of the individual, it is often more desirable to calculate a standardized estimate of the growth rate of insect populations (Southwood 1978). One such estimator, the intrinsic rate of increase \( r_m \), has been used for many years by insect ecologists.

Although the use of \( r_m \) has been criticized (e.g., Hirose 1986, Laughlin 1965) for the assumption of a stable age distribution (see Andrewartha & Birch 1954) in study populations, it has been demonstrated to be both a predictive and comparative measure of population growth potential (e.g., Force 1974, Force & Messenger 1964). This parameter has been used widely in the study of a variety of insect populations (see Gaston 1988). In biological control, this statistic has been used as a bioclimatic index and a natural enemy rating parameter (e.g., Messenger 1964, 1970). It is not only useful for comparing between beneficial species, but also for comparing biotypes of the same species, and for comparing natural enemies to their prey or host (e.g., Force & Messenger 1964, Orphanides & Gonzales 1971, Nichols et al. 1989).

Since \( r_m \) is an estimate, it is important to recognize the uncertainty associated with it. Meyer et al. (1986) introduced a Jackknife estimate of the variance of \( r_m \), which can be used to assess this uncertainty. However, the calculation of \( r_m \) and the variance estimate must be done on a computer, and programs to perform the required computations have not been widely available. Abou-Setta et al. (1986) described a program written in BASIC which calculated fertility table parameters for arthropods, however, the program did not include an estimate of the variance of \( r_m \). In this paper we describe a computer program, written in Pascal, which provides such an estimate in addition to approximate confidence intervals, fertility table parameters with their standard errors, and daily means of progeny production and survivorship.

**Program Description**

In this section we describe program input and output, as well as the computational algorithms used by the program. Mathematical notation is introduced to abbreviate and simplify the discussion. No details on program operation are included.

Input and Output

Input to the program consists of data from on or more replications (cohorts) for a particular population. Each line of input consists of: a replication number \( i \), animal number within the replication \( j \), a pivotal age \( x \) (see Birch 1948, and example in this paper), the number of female offspring of the \( j^{th} \) animal at age \( x \) \( \eta_{ijx} \), and the number of male offspring of the \( j^{th} \) animal at age \( x \) \( \eta_{ijx} \). After this data has been inputted, the program will ask for the pre-imago survivorship \( S_0 \) (see Fig. 1).

Output is produced for each replication, and for all replications combined. The following quantities are included: intrinsic rate of increase \( r_m \), a Jackknife estimate of \( r \) \( r_j \) an estimate of the standard error of \( r_j \) \( \sigma_r \), a confidence interval for \( r \), fertility table parameters (longevity, total progeny production, net reproductive rate \( R_n \), mean generation time, doubling time, pre-ovipositional and post-ovipositional periods) and a table of daily means (mean number of female progeny per adult female \( m_x \), survivorship \( l_x \) mean number of male progeny per adult female, percent females). Additionally, approximate standard errors for the estimates of total progeny production, \( R_n \), longevity, and pre- and post-ovipositional periods are included.

In the following two sections we describe the calculation of the quantities and comment on the interpretation of the output. The program also accepts a table of \( x \), \( m_x \) and \( l_x \) values as input, but in that case, not all of the output quantities can be computed. In particular, \( \sigma_j \) is unavailable.
**** Population Growth Rate Analysis Program ****

Animal Name: Species A  
Temperature: 70 F  
Time interval: 1 day  
Preimaginal Survivorship: 0.90  
Confidence Level for Intervals: 0.95

**** For All Cohorts Combined ****

Number of Individuals: 10

<table>
<thead>
<tr>
<th>X</th>
<th>Mx</th>
<th>Lx</th>
<th>Males</th>
<th>% Females</th>
</tr>
</thead>
<tbody>
<tr>
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<td>3.80</td>
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</tr>
<tr>
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<td>0.09</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Complete Data Estimate $r$: 0.199  
Jacknife Estimate of $r$: 0.204  
Std Error of Jacknife Estimate: 0.030  
Interval Estimate for $r$: [0.136, 0.271]

Adult Longevity: 7.00 (0.615)  
Total Progeny Production: 16.02 (1.546)  
Net Reproductive Rate: 10.35 (1.100)  
Sex Ratio (% Females): 63.81  
Mean Conformation Time: 11.77  
Doubling Time: 3.49  
Pre-Ovipositional Period: 0.00 (0.000)  
Post-Ovipositional Period: 1.50 (0.373)  
Finite Rate of Increase: 1.22

**** For Cohort 1 ****

Number of Individuals: 5

<table>
<thead>
<tr>
<th>X</th>
<th>Mx</th>
<th>Lx</th>
<th>Males</th>
<th>% Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>10.5</td>
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<td>0.90</td>
<td>1.60</td>
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</tr>
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<td>0.90</td>
<td>1.00</td>
<td>58.33</td>
</tr>
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<td>0.75</td>
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<td>0.18</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Fig. 1. Program output for data presented in Tables 1 and 2.
Complete Data Estimate of $r$: 0.199  
Jackknife Estimate of $r$: 0.200  
Std Error of Jackknife Estimate: 0.015  
Interval Estimate for $r$: [0.159, 0.241]  

Adult Longevity: 7.40 (1.030)  
Total Progeny Production: 16.20 (2.745)  
Net Reproductive Rate: 10.44 (2.084)  
Sex Ratio (% Females): 62.31  
Mean Generation Time: 11.81  
Doubling Time: 3.49  
Pre-Ovipositional Period: 0.00 (0.000)  
Post-Ovipositional Period: 1.80 (0.735)  
Finite Rate of Increase: 1.22

***** For Cohort 2 *****

Number of Individuals: 5

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<th>$M_X$</th>
<th>$L_X$</th>
<th>Males</th>
<th>% Females</th>
</tr>
</thead>
<tbody>
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<td>1.00</td>
<td>58.33</td>
</tr>
<tr>
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<td>40.00</td>
</tr>
<tr>
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<td>0.18</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Complete Data Estimate of $r$: 0.190  
Jackknife Estimate of $r$: 0.199  
Std Error of Jackknife Estimate: 0.009  
Interval Estimate for $r$: [0.175, 0.223]  

Adult Longevity: 6.60 (0.748)  
Total Progeny Production: 15.84 (1.791)  
Net Reproductive Rate: 10.26 (1.050)  
Sex Ratio (% Females): 65.31  
Mean Generation Time: 11.73  
Doubling Time: 3.49  
Pre-Ovipositional Period: 0.00 (0.000)  
Post-Ovipositional Period: 1.20 (0.200)  
Finite Rate of Increase: 1.22

Fig. 1. (continued)
Population Growth Rate Analysis Program

Animal Name: Species B
Temperature: 70 F
Time Interval: 1 day
Preimaginal Survivorship: 0.70
Confidence Level for Intervals: 0.95

For All Cohorts Combined

Number of Individuals: 10

<table>
<thead>
<tr>
<th>X</th>
<th>Mx</th>
<th>Lx</th>
<th>Males</th>
<th>% Females</th>
</tr>
</thead>
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</tr>
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<td>0.60</td>
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<td>0.80</td>
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<td>0.14</td>
<td>1.00</td>
<td>0.00</td>
</tr>
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</table>

Complete Data Estimate of r: 0.085
Jackknife Estimate of r: 0.087
Std Error of Jackknife Estimate: 0.015
Interval Estimate for r: [0.053, 0.122]

Adult Longevity: 7.60 (0.670)
Total Progeny Production: 15.05 (2.021)
Net Reproductive Rate: 7.63 (1.056)
Sex Ratio (% Females): 51.65
Mean Generation Time: 24.04
Doubling Time: 8.20
Pre-Ovipositional Period: 1.70 (0.153)
Post-Ovipositional Period: 0.30 (0.153)
Finite Rate of Increase: 1.09

For Cohort 1

Number of Individuals: 5

<table>
<thead>
<tr>
<th>X</th>
<th>Mx</th>
<th>Lx</th>
<th>Males</th>
<th>% Females</th>
</tr>
</thead>
<tbody>
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</tr>
</tbody>
</table>

Fig. 1. (continued)
Complete Data Estimate of r: 0.084  
Jacknife Estimate of r: 0.085  
Std Error of Jacknife Estimate: 0.009  
Interval estimate for r: [ 0.060, 0.109 ]

Adult Longevity: 7.40 (7.166)  
Total Progeny Production: 14.56 (3.353)  
Net Reproductive Rate: 7.56 (1.804)  
Sex Ratio (% Females): 53.16  
Mean Generation Time: 24.18  
Doubling Time: 8.28  
Pre-Ovipositional Period: 1.60 (0.245)  
Post-Ovipositional Period: 0.40 (0.245)  
Finite Rate of Increase: 1.09

***** For Cohort 2 *****

Number of Individuals: 5

<table>
<thead>
<tr>
<th>X</th>
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<th>% Females</th>
</tr>
</thead>
<tbody>
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<td>0.00</td>
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<tr>
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<td>0.70</td>
<td>0.20</td>
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<td>0.42</td>
<td>0.67</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Complete Data Estimate of r: 0.085  
Jacknife Estimate of r: 0.086  
Std Error of Jacknife Estimate: 0.007  
Interval Estimate for r: [ 0.067, 0.105 ]

Adult Longevity: 7.80 (0.800)  
Total Progeny Production: 15.54 (2.651)  
Net Reproductive Rate: 7.70 (1.328)  
Sex Ratio (% Females): 50.13  
Mean Generation Time: 23.90  
Doubling Time: 8.12  
Pre-Ovipositional Period: 1.80 (0.200)  
Post-Ovipositional Period: 0.20 (0.200)  
Finite Rate of Increase: 1.09

Fig. 1. (continued)
Computational Details

In what follows we will drop the "i" subscript and assume we are working with a particular replication (or a new "replication" formed from all individuals in all replications). Define, for a given replication:

\[ n = \text{number of individuals in the replication} \]
\[ x_o = \text{preimaginal development time} \]
\[ \Omega = \text{maximum age among the } n \text{ individuals}, \]
\[ \Omega_j = \text{age at death for the } j^{th} \text{ individual}, \]
\[ \tau_{ix} = \begin{cases} 1 & \text{if } j^{th} \text{ individual is alive at age } x \\ 0 & \text{otherwise} \end{cases} \]
\[ x_j^{(1)} = \text{age at which } j^{th} \text{ individual produces first progeny} \]
and
\[ x_j^{(2)} = \text{age at which } j^{th} \text{ individual produces last progeny}. \]

\[ m_x = \left( \sum_{j=1}^{n} \tau_{jx} \right)^{-1} \sum_{j=1}^{n} \eta_{jx} \]

\[ l_x = \left( \sum_{j=1}^{n} \tau_{jx} \right) \left( \frac{\pi_o}{\sum_{j=1}^{n} \tau_{jx} x_o} \right) = \left( \frac{\pi_o}{n} \right) \left( \sum_{j=1}^{n} \tau_{jx} \right) \]

\[ \text{adult longevity} = \frac{1}{n} \sum_{j=1}^{n} \left( \sum_{x=x_o}^{\Omega} \tau_{jx} \right) \]

\[ \text{total progeny production per adult female} = \frac{1}{n} \sum_{j=1}^{n} \left( \sum_{x=x_o}^{\Omega} \eta_{jx} + N_{jx} \right) \]

\[ R_o = \frac{\pi_o}{n} \sum_{j=1}^{n} \left( \sum_{x=x_o}^{\Omega} \eta_{jx} \right) = \sum_{x=x_o}^{\Omega} \left( \frac{\pi_o}{n} \sum_{j=1}^{n} \tau_{jx} \right) = \sum_{x=x_o}^{\Omega} l_x m_x \]

\[ \text{daily sex ratio} = \frac{\sum_{j=1}^{n} \eta_{jx}}{\sum_{j=1}^{n} \left( \eta_{jx} + N_{jx} \right)} \]

\[ \text{overall sex ratio} = \sum_{j=1}^{n} \left[ \frac{\sum_{x=x_o}^{\Omega} \eta_{jx}}{\sum_{x=x_o}^{\Omega} \left( \eta_{jx} + N_{jx} \right)} \right] \]

\[ \text{mean generation time} = \frac{\ln(R_o)}{r_m} \]
\[ \text{doubling time} = \frac{\ln(2)}{r_m} \]
pre-ovipositional period = \frac{1}{n} \sum_{j=1}^{n} \left( x_j^{(1)} - x_o \right) \\
and \\
post-ovipositional period = \frac{1}{n} \sum_{j=1}^{n} \left( \Omega_j - x_j^{(2)} \right)

Note that adult longevity, \( R_o \), total progeny production, and pre- and post-ovipositional period can be written as

\[ \bar{y} = \frac{1}{n} \sum_{j=1}^{n} y_j \]

for suitably defined "y" (e.g., for longevity, \( y_j = \sum_{x=x_o}^{\infty} \tau_{jx} \)). An estimated standard error for these quantities is calculated as

\[ \sqrt{\frac{1}{n(n-1)} \sum_{j=1}^{n} (y_j - \bar{y})^2}. \]

The intrinsic rate of increase, \( r_m \), is defined as the solution to

\[ 1 = \sum_{x=x_o}^{\infty} e^{-rx} l_x m_x \]

which is a nonlinear equation in \( r \). We solve Equation 1 using the Dekker-Brent method (Press et al. 1986), a general-purpose, derivative-free method for solving nonlinear equations in a single variable. The procedure requires two initial values for \( r \) which bracket the solution—we use 0 and 1. The finite rate of increase is calculated as \( e^r \).

The Jackknife (Tukey 1958) is a general nonparametric procedure for obtaining estimated standard errors for statistics which are complex functions of the data. Meyer et al. (1986) use the jackknife to obtain standard errors for intrinsic rates of increase. A brief description of the technique follows.

Let \( r_m \) be the solution to Equation 1 obtained using all the data, and let \( r_{mj}(j = 1, \ldots, n) \) be the solution to Equation 1 obtained after dropping individual \( j \) out of the data set. Then the Jackknife "pseudo-values" are computed as

\[ \bar{r}_j = n r_{mj} - (n - 1) r_m. \]

The pseudo-values are used to construct a new point estimate of \( r \)

\[ \hat{r}_J = \frac{1}{n} \sum_{j=1}^{n} \bar{r}_j \]

and an estimate of the standard error of \( \hat{r}_J \)

\[ \hat{\sigma}_J = \sqrt{\frac{1}{n(n-1)} \sum_{j=1}^{n} (\bar{r}_j - \hat{r}_J)^2}. \]
If we assume that the \( \hat{r}_j \) are independent draws from an approximately normal distribution with mean \( r \), an approximate \( 100(1 - \alpha)\% \) confidence interval for \( r \) is given by

\[
\hat{r}_J \pm t_{v, \frac{\alpha}{2}} \cdot \hat{\sigma}_J
\]

where \( v = n-1 \) and \( t_{v, \frac{\alpha}{2}} \) is the upper-\( \frac{\alpha}{2} \) point of the Students t-distribution with \( v \) degrees of freedom. In this program, the value of \( t_{v, \frac{\alpha}{2}} \) is obtained using the procedure of Koehler (1983).

Interpretation of Output

The confidence interval provided by the program enables the user to draw conclusions about the true \( r \) value for the particular species under consideration. Note that the interval is approximate; an assessment of the performance of the interval for cladoceran (Daphnia pulex DeGeer) populations is given in Meyer et al. (1986).

The output from the program can also be used to statistically compare \( r_m \) values for two or more populations (species, biotypes, etc.). First consider the comparison of two species. Let \( \hat{r}^{(1)}_J \) and \( \hat{\sigma}^{(1)}_J \) be the Jackknife estimates for species 1 and let \( \hat{r}^{(2)}_J \) and \( \hat{\sigma}^{(2)}_J \) be the estimates for species 2 (all numbers would be taken from the program output). Now if \( r^{(1)} \) and \( r^{(2)} \) are the true population growth rates for the species, then an approximate \( 100(1 - \alpha)\% \) confidence interval for \( r^{(1)} - r^{(2)} \) is

\[
\hat{r}^{(1)}_J - \hat{r}^{(2)}_J \pm t_{f, \frac{\alpha}{2}} \sqrt{\left(\frac{(\hat{\sigma}^{(1)}_J)^2}{f} + \left(\frac{(\hat{\sigma}^{(2)}_J)^2}{f}\right)^2\right)}
\]

\[
\hat{r}^{(1)}_J - \hat{r}^{(2)}_J \pm t_{f, \frac{\alpha}{2}} \sqrt{\left(\frac{(\hat{\sigma}^{(1)}_J)^2}{f} + \left(\frac{(\hat{\sigma}^{(2)}_J)^2}{f}\right)^2\right)}
\]

\[
\hat{r}^{(1)}_J - \hat{r}^{(2)}_J \pm t_{f, \frac{\alpha}{2}} \sqrt{\left(\frac{(\hat{\sigma}^{(1)}_J)^2}{f} + \left(\frac{(\hat{\sigma}^{(2)}_J)^2}{f}\right)^2\right)}
\]

\[
\hat{r}^{(1)}_J - \hat{r}^{(2)}_J \pm t_{f, \frac{\alpha}{2}} \sqrt{\left(\frac{(\hat{\sigma}^{(1)}_J)^2}{f} + \left(\frac{(\hat{\sigma}^{(2)}_J)^2}{f}\right)^2\right)}
\]

\[
\hat{r}^{(1)}_J - \hat{r}^{(2)}_J \pm t_{f, \frac{\alpha}{2}} \sqrt{\left(\frac{(\hat{\sigma}^{(1)}_J)^2}{f} + \left(\frac{(\hat{\sigma}^{(2)}_J)^2}{f}\right)^2\right)}
\]

\[
\hat{r}^{(1)}_J - \hat{r}^{(2)}_J \pm t_{f, \frac{\alpha}{2}} \sqrt{\left(\frac{(\hat{\sigma}^{(1)}_J)^2}{f} + \left(\frac{(\hat{\sigma}^{(2)}_J)^2}{f}\right)^2\right)}
\]

where

\[
f = \frac{\left[\left(\frac{(\hat{\sigma}^{(1)}_J)^2}{f}\right) + \left(\frac{(\hat{\sigma}^{(2)}_J)^2}{f}\right)\right]^2}{\frac{(\hat{\sigma}^{(1)}_J)^4}{n_1-1} + \frac{(\hat{\sigma}^{(2)}_J)^4}{n_2-1}}
\]

and \( n_1 \) and \( n_2 \) are the number of animals in the data sets from species 1 and 2, respectively. The degrees of freedom approximation \( f \) is that proposed by Satterthwaite (1946). Intervals of the form (2) are discussed by Snedecor and Cochran (1980, sec. 6.11). Note that \( f \) may not be an integer; it should be rounded off for use with a t-table. Conservative intervals may be obtained by replacing \( f \) with \( \frac{n_1+n_2}{2} - 1 \). An interval which does not include 0 can be viewed as evidence of a difference between the \( r \) values of the two species. As in the last section, this interval is based on assumptions of independence and approximate normality.

The above interval should be used to make specific pairwise comparisons. If more than two species are being considered, and it is desired to make all pairwise comparisons, a multiple comparisons procedure must be used. There are many such procedures, one choice is the Newmann-Keuls sequential test. This test requires the calculation of a Q-statistic for different sets of species (see Snedecor and Cochran 1980, sec. 12.13 for details on the procedure). Here we indicate how to compute the Q-statistic for a given set of species. Specifically, consider species \( 1, 2, \ldots, k \). Let \( \hat{r}_J^{(1)}, \ldots, \hat{r}_J^{(k)} \) be the Jackknife estimates of the population growth rates. Further, let \( \hat{r}_J^{(A)} \) be the maximum and \( \hat{r}_J^{(B)} \) be the minimum of \( \hat{r}_J^{(1)}, \ldots, \hat{r}_J^{(k)} \) and let \( \hat{\sigma}_J^{(A)} \) and \( \hat{\sigma}_J^{(B)} \) be the associated standard errors. Then the Q-statistic is calculated as
\[
Q = \frac{\bar{r}_J(A) - \bar{r}_J(B)}{\sqrt{(\sigma_J(A))^2 + (\sigma_J(B))^2}};
\]

its associated degrees of freedom are \( \frac{n_A + n_B}{2} - 1 \).

Example

In the following example, we compare two hypothetical species (A and B) of parasitic wasps. Species A has a mean preimaginal developmental time of 10 days and preimaginal survivorship of 0.90; species B has corresponding values of 20 days and 0.70, respectively. Note that this data could be from previous studies or could be collected from the \( r_m \) study population. Also note that although data on male and female progeny production are presented in this example, where this information may be difficult or impossible to collect it may be necessary to multiply progeny production values by the total population sex ratio to obtain \( m_x \) values.

Tables 1 and 2 present 'raw data' for two cohorts (or replications) for each species. Program output is given in Figure 1. In this example, the population growth rate for Species A is estimated (using both replications) to be 0.20, and an associated confidence interval is \([0.14, 0.27]\) (while the program reports 3 significant figures, we follow the recommendation of Meyer et al. (1986), and report only two significant figures here). The values for Species B are 0.09 and \([0.05, 0.12]\). These results indicate a difference in values between the two species. A better comparison is made using the 95% confidence interval for the difference in \( r \) values. It is

\[
(0.20 - 0.09) \pm (2.16)\sqrt{(0.03)^2 + (0.015)^2}
\]

\[= 0.11 \pm 0.072 \]

\[= [0.038, 0.182]\]

which does not include 0. Thus we would conclude that the population \( r \) values are different. For this interval we used degrees of freedom.

<p>| TABLE 1. Progeny production (♀,♂) by two cohorts (replications) of hypothetical parasitoid species A (D=day parasitoid was found dead). |
|---|---|---|---|---|---|---|---|---|---|
| Adult Age (d) | Pivotal Age (d) | COHORT I | | | | | | | |
| | | ♀1 | ♀2 | ♀3 | ♀4 | ♀5 | ♀1 | ♀2 | ♀3 | ♀4 | ♀5 |
| 1 | 10.5 | 5.1 | 6.2 | 2.2 | 3.1 | 3.2 | 4.2 | 3.1 | 5.2 | 3.2 | 4.1 |
| 2 | 11.5 | 4.1 | 3.1 | 1.2 | 4.1 | 3.1 | 3.1 | 2.1 | 4.1 | 3.1 | 2.1 |
| 3 | 12.5 | 2.0 | 3.2 | 1.1 | 3.1 | 2.1 | 3.1 | 3.1 | 2.2 | 2.1 | 2.1 |
| 4 | 13.5 | 2.1 | 2.2 | 0.0D | 2.1 | 1.1 | 2.1 | 1.1 | 2.1 | 1.1 | 1.1 |
| 5 | 14.5 | 0.1 | 1.1 | | 1.1 | 0.0 | 1.1 | 0.0D | 0.1 | 0.1 | 0.0D |
| 6 | 15.5 | 0.0 | 0.0 | 2.1 | 0.0 | 0.1 | 0.0 | 0.0 | 0.1 | 0.1 | 1.1 |
| 7 | 16.5 | 0.1D | 0.0 | 1.1 | 0.0D | 0.0D | 0.0D | 0.0D | 1.1 | 0.0 |
| 8 | 17.5 | 0.0 | 0.1 | | 0.0 | 0.0 | 0.0 | 0.0D | 0.0 | 0.0D |
| 9 | 18.5 | 0.0D | 1.1 | | 0.0D | 0.0D | 0.0D | 0.0D | 0.0 | 0.0D |</p>
<table>
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<th>Adult Age (d)</th>
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<th>COHORT II</th>
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</table>

\[ f = \frac{((0.030)^2 + (0.015)^2)^2}{(0.030)^4 + (0.015)^4} = 13.23 \approx 13. \]

In order to test the accuracy of this program, we analyzed data tabulated by Birch (1948) for Sitophilus oryzae (L.) (Coleoptera: Curculionidae). The computed values were the same as those presented by Birch (1948), as follows: \( r_m = 0.762; R_o = 113.48; T = 6.21 \).

This program can be run on IBM PC-compatible microcomputers or DEC VAX minicomputers. A copy of the compiled program (for IBM compatibles) or the program code will be provided along with a manuscript reprint if a formatted 5¼ in. diskette is sent to any of the authors. The program is written in standard Pascal, so it can be compiled on a wide variety of computers. The program has been run on IBM compatible microcomputers, DEC VAX minicomputers and Sun workstations.

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