A Method for Determining the Intrinsic Rate of Natural Increase
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The intrinsic rate of natural increase \( r_m \) is an important population parameter used to measure the population growth potential of a species under specified conditions. Given fertility and survivorship data, \( r_m \) is calculated from

\[
\sum_{x=0} \sum_{a=0} m_{a|x} \exp(-r_m x) = 1, \quad (1)
\]

where \( x \) is the pivotal age for the age class in units of time, \( m_{a|x} \) is the number of females born per female in each age interval, and \( l_x \) is the proportion of females that survive to age \( x \).

Several authors have introduced calculation procedures, as follows:

1) An approximate value of \( r_m \), called \( r_0 \), is obtained by the formula

\[
r_0 = \frac{(\sum m_{a|z})(\ln \sum m_{a|z})}{\sum x m_{a|z}}, \quad (2)
\]

(for example, see Irô, 1963; Irô and Murai, 1977; Morisita, 1961; Pianka, 1978).

2) Taking \( r_0 \) as a possible value of \( r_m \), two trial values are selected on either side of it. Then, \( r_m \) is estimated graphically by plotting the two trial values of \( r_m \) against the sums defined by the next formula (Southwood, 1966).

\[
\sum_{x=0} \sum_{a=0} (\sum m_{a|x}) \exp(-r_m x) \cdot m_{a|x} = 0 \quad (3)
\]

3) Using the relationship between \( r_m \) and \( r_0 \) (Southwood, 1978);

\[
r_0 = r_m \left(1 - \frac{r_m \sigma^2}{2T_0^2} + \ldots \right), \quad (4)
\]

where \( T_0 \) is the cohort generation time and \( \sigma^2 \) is the variance of the \( m_{a|x} \) distribution; and these are defined as:

\[
T_0 = \sum x m_{a|x} \sum m_{a|x} \quad (5)
\]

and

\[
\sigma^2 = \sum x^2 m_{a|x} \sum m_{a|x} - T_0 \quad (6)
\]

Higher order moments are omitted from Eq. (4), but it is exact when the \( m_{a|x} \) distribution is normal (Southwood, 1978).

4) By a trial and error process substituting values into \( r_m \) in Eq. (1) until a suitable approximate value is found (Elseth and Baumgardner, 1981; Piérou, 1974). Piérou (1974) suggested obtaining \( r_0 \) to find a good first trial value.

5) By plotting the sum \( \sum \sum \exp(m_{a|x}) \) as a function of \( r \) and drawing a line through the points, \( r_m \) is estimated graphically as the point at which the sum is unity (Ricklefs, 1982).

As Eq. (4) implies, the first method gives an accurate solution only in a special case; generation is discrete and the birth of offspring occurs at once. Laughlin (1965) has proposed that the value obtained by this method be distinguished as a capacity for increase (Southwood, 1966). The second and third methods aim to obtain an adequate solution by procedures suitable for hand calculation, but they require extensive and tedious operation. The fourth and fifth methods are too laborious to deal with by hand calculation.

The present method shares the same logic with the fourth and fifth methods in solving Eq. (1) and is designed to operate by computer. In comparison, this procedure is more straightforward because it adopts Newton's method. In this \( f(r) \) is a function of \( r \) defined as:

\[
f(r) = \sum \sum m_{a|x} \exp(-r x) \cdot 1. \quad (7)
\]

Differentiating this with respect to \( r \), we have

\[
f'(r) = -\sum \sum x m_{a|x} \exp(-r x). \quad (8)
\]

Since \( f(r) \) has a finite derivative at any point of \( r \), it is a continuous function. Considering the function \( f(r) \) at the point \( r = r_0 \), \( f'(r_0) \) is the slope of \( f(r) \) at this point.

Next, let

\[
g(r) = \alpha + \beta r \quad (9)
\]

be a line passing through a point \( (r_0, f(r_0)) \) and having the slope \( f'(r_0) \). Then, the line intercepts the \( r \)-axis at

\[
r \equiv r_1 = -\alpha / \beta = r_0 - f(r_0) / f'(r_0). \quad (10)
\]

Replacing \( r_0 \) in the above equation with the value obtained for \( r_1 \), second approximate value \( r_2 \) is obtainable. In general, the \( n \)th approximate value \( (r_n) \) of \( r_m \) is given by,

\[
r_m = r_{n-1} - f(r_{n-1}) / f'(r_{n-1}). \quad (11)
\]
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Table 1. The values of $r_m$ estimated by the present method (A) compared with those obtained by the authors (B) referred to in the text

<table>
<thead>
<tr>
<th>Species</th>
<th>$r$ value</th>
<th>Method</th>
<th>Unit of time</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhopalosiphum maidis</td>
<td>0.404</td>
<td>A</td>
<td>1 day</td>
<td>Itô (1963), Itô and Murai (1977)</td>
</tr>
<tr>
<td>Calandra oryzae (29°C)</td>
<td>0.762</td>
<td>B</td>
<td>1 week</td>
<td>Môrisita (1961)</td>
</tr>
<tr>
<td>Ovis aries</td>
<td>0.200</td>
<td></td>
<td>1 year</td>
<td>Piëloû (1974)</td>
</tr>
<tr>
<td>Chydotus sphaericus (15°C)</td>
<td>0.146</td>
<td></td>
<td>1 day</td>
<td>Piëloû (1974)</td>
</tr>
<tr>
<td></td>
<td>0.214</td>
<td></td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

*a Method used to obtain the value in column B; see the text for further explanation.

The value $r_m$ converges to the true value of $r_m$ with iterative calculations. Although an arbitrarily chosen value can be used as a starting value $r_0$, it is better to use the value given by Eq. (2) to avoid extra iterations.

Some of the above authors explained their calculation procedures by presenting fertility and survivorship data with their results. Excepting Itô (1963), however, all adopted data originated by other authors. Using these data the iteration was performed until $|f(r)| \leq 0.00001$ was satisfied. The values obtained were rounded off to three decimal places and are shown in Table 1 together with the authors’ results and their methods used.

In all examples, the values of $r_m$ were smaller than $r_m$ estimated by the present method. This is because the reproductive period is long in these species. The data also showed that the $m_{el}$ distributions were skewed to the right, violating the assumption of normal distribution. This indicates that the solution by Eq. (4) must be verified as to whether or not it sufficiently satisfies. Not surprisingly, the fourth and fifth methods yielded solutions very close to those by the present method.

A computer program written in BASIC is available on request to carry out the rather extensive calculations.

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REFERENCES


