Density Estimation by the Modified JACKSON's Method

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In this study it has been assumed that single batches of marked individuals were released and subsequent density estimates were based on samples obtained by recapture counts which were then removed from the population. The bias in these estimates was calculated by using both JACKSON's positive method and IRÔ's modified method for simulated populations. This author concludes that IRÔ's method is more useful than JACKSON's under conditions of low mortality and low capture rates, and, further, that the degree of negative bias in both these methods tends to increase with increases in rates of mortality and capture. IRÔ's method cannot be applied where the density of wild individuals is extremely low vis-a-vis the marked population. In order to minimize this defect the author proposes a method whereby the ratio of marked to unmarked individuals is used in place of the ratio of marked to total individuals. Another method, usable in situations where the number of captured wild individuals remains nearly constant, to ascertain approximately the rates of survival, capture and density of wild population is also proposed.

INTRODUCTION

Normally the population density of fruit flies is so low and their activity so extensive that it is very difficult to estimate density by direct sampling technique such as sweeping. Furthermore, while the existence of effective male attractants for fruit flies would normally make the application of the 'mark-recapture' method possible, the melon flies, Dacus cucurbitae CoQ., under study seem to show a marked lowering of response to the attractant after one exposure to it (CHAMBERS et al., 1972), so this method was also eliminated.

Under the circumstances, we decided to base our study on a single release in the field of a large number of laboratory-reared flies with subsequent population density estimation figures based on flies caught in bait traps which are then removed permanently from the population. Although there are some methods applicable with this type of procedure (SEBER, 1973), they are all rather complicated.

In order to facilitate density estimation, IRÔ (1973) proposed a system based on JACKSON's positive method using data from a single release and repeated recapture samplings. He stated that there was negative bias inherent in his system influenced by rates of survival and of capture.

In this paper, the bias inherent in IRÔ's system under various simulated conditions has been computed by HITAC 8500 and some improvements in his system are proposed.

METHODS

In this paper the following symbols are used:

U = Initial density of wild (unmarked) population.

\( \hat{U} \) = Estimated density of wild (unmarked) population.
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\[ \hat{N} = \frac{10^4 m_i}{n_i M_0} \]

If the rate of decrease of \( y_i \) is constant, we can calculate \( \hat{y}_0 \), which according to Jackson, is an imaginal value of recapture assuming that 100 marked individuals released instantaneously intermingle with the population and 100 individuals are caught immediately after the release.

From this, population size is estimated as

\[ \hat{N} = \frac{10^4}{\hat{y}_0} \]

Ito (1973) stated that Jackson’s method could be used only where recaptured individuals were returned alive to the original population. He concluded that it was better to use the number of marked individuals surviving at time \( i \), \( M_{0(i)}' \), in place of \( M_0 \) in the case where the captured animals were eliminated.

That is,

\[ M_{0(i)}' = M_0 - \sum_{j=1}^{i-1} M_j \]
\[ y_i' = \frac{10^4 m_i}{n_i M_{0(i)}'} \]

He also recommended the use of the regression method for computation of \( y_0' \) in place of Jackson’s equation. That is,

\[ \log y_i' = \log \hat{y}_0' + i \log S \]

Estimates of \( N \) can be obtained using \( \hat{y}_0' \) instead of \( \hat{y}_0 \) in equation (2).

\[ \hat{N} = \frac{10^4}{\hat{y}_0'} \]

The validity of this method is checked by using a simulation technique with the following assumptions similar to Ito’s (1973).

1. In a wild population, birth rate is equal to natural mortality and death on capture is compensated for by dilution (immigration).
2. The survival rate of marked individuals is constant.
3. The rate of capture is constant and the same for both marked and unmarked populations.

The bias of estimates is calculated using the following values for four factors respectively.
1. Population densities of marked and unmarked population:
   1) \( U = 10^4, M_0 = 10^3 \)  
   2) \( U = M_0 = 10^4 \)  
   3) \( U = 10^3, M_0 = 10^4 \).
2. Survival rate of marked individuals: \( S = 0.95, 0.9, 0.85. \)
3. Rate of capture: \( R = 0.05, 0.1, 0.15. \)
4. Number of samples: 4 or 6.

Under the assumptions above, the values of \( u_i \) and \( m_i \) are given as follow,
\[
  u_i = U \cdot R \quad \text{(constant for all } i \text{'s)}
\]
and
\[
  m_i = M_i R
\]
where
\[
  M_i = M_0 S
\]
and
\[
  M_i = M_i-1 S(1-R) \quad (i \geq 2)
\]
Accordingly, \( M_i \) is calculated as follows,
\[
  M_i = M_0 S^i (1-R)^{i-1}
\]

Using simulated values for \( u_i, m_i \) and \( M_i \), the values of \( y_0 \) and \( y_0' \) are computed by linear regression and the total number of marked and unmarked individuals, \( \hat{N} \), can be obtained by using equation (2) or (6).

Finally, the density of the wild population is computed by subtracting \( M_0 \) from \( \hat{N} \).

The bias is shown by the percentage of the estimated number to the true number in the wild population.

RESULTS AND DISCUSSION

Density estimation by Jackson’s method and Ito’s modified method

Bias in the estimation of size of the wild population by Jackson’s method and Ito’s modified method are indicated in columns ‘Method A’ and ‘Method B’ in Table 1, respectively. It is obvious that where the density of wild flies is not smaller than that of marked flies, the estimates by Ito’s method are consistently better than those arrived at by Jackson’s method, whatever the values of survival rate and the rate of capture. The negative bias of estimates by Jackson’s method increases when the number of marked individuals is similar to that of unmarked individuals. On the other hand, the degree of negative bias produced by using the modified method is not as great even when the number of marked individuals is similar to the number of unmarked ones. It may be expected from results shown in Table 1 that the negative bias in Ito’s method does not exceed 10% under the conditions where rates of mortality and capture are under 0.15, as long as the first several values of \( y_i \) are used for calculation. Thus, the modification made by Ito (1973) to Jackson’s method seems to be appropriate.

The negative bias by Jackson’s method is still greater when the majority of sampled individuals are marked ones (\( U \ll M_0 \)) than when \( U \gg M_0 \) and \( U \approx M_0 \). The bias in the modified method, on the other hand, becomes positive if \( U \ll M_0 \), which is usually
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Table 1. Bias of Estimated Density by Three Methods Against True Density Shown by Percentage

<table>
<thead>
<tr>
<th>Methods</th>
<th>A</th>
<th>B</th>
<th>C</th>
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<tbody>
<tr>
<td>S</td>
<td>4b</td>
<td>6b</td>
<td>4b</td>
</tr>
<tr>
<td>0.05</td>
<td>95.5</td>
<td>96.1</td>
<td>100.2</td>
</tr>
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<td>0.10</td>
<td>90.3</td>
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<td>96.1</td>
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<td>98.1</td>
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<td>98.5</td>
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<td>88.9</td>
<td>96.8</td>
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<td>92.6</td>
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<td>142.3</td>
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</table>

a A, Jackson's method; B, Irô's modified method; C, A method using the index $x_i'$.  
b The figures indicate the number of sampling.

the case when a number of marked sterile males are released for practical purposes and estimation of the number of wild flies is attempted by using the recapture data.

In this case, as $m_i$ is remarkably larger than $u_{it}$, $m_i/(u_{it}+m_i)$ in equation (4) approaches unity. Consequently, the value of $y_i'$ is largely determined by the values of $1/M_{0(0)}'$. $M_{0(0)}'$ decreases rapidly and the value of $y_i'$ becomes larger than that of $y_i$. Accordingly, $y_i'$ is underestimated and the density of the wild population is overestimated.

Moreover, when the survival rate is low, the coefficient of determination from the regression of $y_i'$ on time becomes low and the bias of estimates changes irregularly according to the length of sampling chains included in the calculation. It becomes...
necessary to reduce this defect.

An improvement to exclude the influence of the ratio of marked to unmarked population from the estimates

As mentioned in the previous section, \( y_t' \) is strongly influenced by the ratio of \( M_0 \) to \( U \) because this index included the ratio of \( M_t \) to \( M_0 + U_t \). To avoid this effect, we should use the ratio of \( M_t \) to \( U_t \) rather than that of \( M_t \) to \( n_t \). Then a new index, \( z_t' \), which includes the ratio of \( M_t \) to \( U_t \), is defined as below,

\[
z_t' = \frac{10^4 M_t}{U_0 M_0}
\]

(12)

If the rate of decrease of \( z_t \) is constant as in the case of \( y_t \), one can calculate \( z_0' \). This value is the imaginal value of recapture when one assumes that 100 marked individuals released instantaneously intermingle into the population and one takes samples which include 100 unmarked individuals immediately after the release. We are interested in a situation where captured individuals are removed from the population. Thus, using \( M_{0(t)}' \) instead of \( M_0 \), an index, \( z_t' \), is defined by,

\[
z_t' = \frac{10^4 M_t}{U_0 M_{0(t)}'}
\]

(13)

After estimation of \( z_0' \) by linear regression, the density of wild population is estimated by,

\[
\hat{U} = \frac{10^4}{\frac{z_0'}{2}}
\]

(14)

In the same way as mentioned previously, the density estimation is simulated by using \( z_t' \) and the results are shown in the right column, 'Method C', in Table 1. The results obtained are satisfactory even when the marked individuals dominate. The survival rate and the rate of capture influence is estimated in the same way as that by Ito's modified method. The estimates by this procedure, however, are not influenced by the proportion of marked individuals to wild ones and are not as biased, even when the later samples are included in calculations.

An approximate method for calculating the survival rate, the rate of capture and the number of wild individuals

As mentioned previously, \( m_t \) and \( u_t \) are given by equations (7), (8) and (11). Accordingly, the general form of \( z_t \) can be written as follows:

\[
\hat{z}_t = \frac{10^4 M_0 S'(1-R)^{t-1} R}{U \cdot R \cdot M_0} = \frac{10^4 S'(1-R)^{t-1}}{U}
\]

(15)

When plotting log \( z_t \) against time \( t \), a linear relationship is expected with the slope of log \( S(1-R) \) and the intercept of log \( (10^4/U(1-R)) \). That is to say, the expected value of \( z_0 \) is,

\[
\hat{z}_0 = \frac{10^4}{U(1-R)}
\]

(16)

and the estimate is given by,

\[
\hat{U} = \frac{10^4}{\hat{z}_0} = U(1-R)
\]

(17)

Thus the estimates obtained by this method are biased depending upon the rate of
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Now, if either the survival rate or the rate of capture is known by other means, the density of wild populations is estimated in the following way. With the rate of capture known, the density of wild individuals is,

\[ U = \frac{\bar{U}}{1-R} \]  \hspace{1cm} (18)

With the survival rate known,

\[ U = \frac{\bar{U} \cdot S}{S(1-R)} \]  \hspace{1cm} (19)

where the value of \( S(1-R) \) in the denominator can be obtained from the regression of \( \log z_i \) on time \( i \).

However, since both the factors are usually not known, equations (18) and (19) cannot be applied in estimations of density. An approximate method may be used instead, for example, if the size of wild population is not affected by death on capture because dilution through immigration and birth is balanced with emigration and death and the rate of capture is constant, the captured number of wild individuals, \( u_i \), is constant and equals \( U \cdot R \). (This may be expected when the rate of capture is low, the movement is active to compensate the effect of removal, and the period of release-recapture experiment is short.) So the true value is obtained by summing \( u_i \) and \( \bar{U} \). Practically, the mean of \( u \) should be used. Namely,

\[ \bar{U} + \bar{u} \approx U(1-R) + U \cdot R \]  \hspace{1cm} (20)

Rate of capture is obtained by dividing the mean of \( u_i \) by \( U \). The survival rate can also be calculated by using the rate of capture calculated and the regression coefficient.

A numerical example. Mark-recapture data on the melon fly, *Dacus cucurbitae* Coq., in Ishigaki Is., Okinawa Prefecture (Iro et al., 1974) is summarized in Table 2. In this case, marked flies were released twice at each station and hence Jolly's stochastic model (Jolly, 1965) could be applied for estimation at the time of the second release. Being estimated by Iro's modified method, the densities of wild males at time 0 and time 1 are 2059 and 623 at station C, and 478 and a 'negative number' at station D. By Jolly's model, the estimates at time 1 are 983 and 480 at station C and D, respectively. In this example, the number of unmarked individuals, \( u_i \), did not change notably and hence the method proposed here can be applied. The means of \( u_i \) are 131 and 127 in station C and D, respectively. Logarithm of \( z_i \) is plotted against \( (i-0.5) \) in place of \( i \) because this data was not sampled at time \( i \) but at the interval of time be-

<table>
<thead>
<tr>
<th>Date</th>
<th>Station C</th>
<th>Station D</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unmarked</td>
<td>Red</td>
</tr>
<tr>
<td>June 14/15</td>
<td>1108</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>202</td>
<td>63</td>
</tr>
<tr>
<td>25</td>
<td>197</td>
<td>28</td>
</tr>
<tr>
<td>30</td>
<td>77</td>
<td>1</td>
</tr>
<tr>
<td>July 5</td>
<td>84</td>
<td>2</td>
</tr>
<tr>
<td>127</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>104</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>

*Italic* figures show the number marked and released (After Iro et al. 1974).
between \((i-1)\) to \(i\). The first three or four values of \(z_i\) are used for calculations to assure the application of the method. The results obtained are shown in Table 3. In all cases the coefficients of determination from the regression are very high \((r^2>0.92)\). Accordingly, the constancy of \(S(1-R)\) is verified, at least approximately. From the values of \(U\) in Table 3, it seems likely that the density is fairly constant at both times. The area in station C is 4 ha and that in station D is 2 ha. Thus the area of the former station is two times as large as the area of the latter but the number of traps set up is the same in both areas. Accordingly, the rate of capture in station D is expected to be two times as high as that in station C. The figures of R shown in Table 3 support this expectation. On the other hand, the survival rates of marked flies in the four cases may be influenced by the differences of released flies between the two releases. In spite of these influences the figures obtained are rather similar to each other.

The number of wild flies at station C is about twice that at station D. Accordingly, the density per ha is similar at both stations, that is, 300 per ha. Twenty-five traps were used in this experiment in each station. At station C the number of traps per ha was about six and the rate of capture per five days was about 0.1 as shown in Table 3. Consequently, rough estimation of the density of wild flies can be obtained by multiplying the mean number of wild insects per trap per five days by sixty.

As with Iro's modified method, the following two conditions must be satisfied for the application of this simple method. One, the number of unmarked individuals caught should be about the same during the mark-recapture experiment. Two, the relationship between \(\log z_t\) and time \(i\) should be linear. Actually, condition one may not be fully satisfied, because the rate of capture must suffer from changes in weather, especially in the case where the subject is caught by an attractant as in our fruit fly research. Moreover, during the later period of the survey density of the wild populations is not sufficiently compensated for by dilution from surrounding areas, because the pressure of capture on the wild population accumulates with time. To avoid this difficulty, it is necessary that data obtained at the later intervals be excluded from calculations and that the mean of \(u_t\) is calculated after excluding extremely low values.

To summarize, the method which uses the index \(z_i\) can be more generally applied than the method using index \(z_t\). But the bias of the estimate by the former method cannot be assessed when the survival rate and the rate of capture are unknown. The
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latter method is useful but can be applied only where the number of wild individuals caught is constant, i.e., the density of wild flies is constant and death on capture does not affect the population density significantly.

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REFERENCES


