# A C T A THERI OLD GI C A 

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The Analysis of Data Obtained from Small Mammal Index Trappings


#### Abstract

The usefulness of the index trapping method for the estimation of small mammal population densities has deen debated, and although the technique has been criticised in the literature, it clearly has its uses for certain limited purposes. One of its drawbacks has been a lack, in the past, of a simple method of comparing two indices, in order to obtain an estimate of the significance of any difference which they may show. This paper suggests a mathematical technique by which paired data obtained from trapping samples may be examined in terms of total catch, individual species between samples, or pairs of species within samples, in order to obtain estimates of significance. Some specific examples are worked out, and attention is drawn to a number of practical considerations which are of importance in collecting data for analysis.


## 1. INTRODUCTION

There are many situations in which some kind of information about small mammal numbers is required, but the time, finance and expertise necessary to carry out a full population estimation are not available. A relative estimate, or index, must then suffice. This, while providing no information about absolute numbers, will provide values which can be compared with other values obtained by the same standard method at another time or place, and so used to assess similarities or differences in animal population densities.

Because small mammal index trapping is relatively easy to carry out, and has proved useful, it has continued to be used despite considerable cricitism (see references quoted by Hansson , 1967). Moreover, the index has been defended by Southern $(1965,1973)$, Hansson (1967) and Linn (1954, 1963). Criticisms of index methods are mainly based on the undoubted fact that it is difficult (and some believe impossible) to devise a field technique in which the capture rates for all individuals of all species, of both sexes, of all ages, under all weather
circumstances, at all seasons, reflect accurately the appropriate population levels. Generations of field workers, comparing data from many different sources, are aware that variations in trappability between individuals exist, and that these variations bedevil any attempt to collect population data on small mammals which will be acceptable for mathematical analysis.

It is, perhaps, easier to approach the ideal of equal trappability when carrying out intensive programmes aimed at making full population estimates, but more difficult to do this in an index trapping when the trapping effort, for various reasons, has to be kept small. As has been implied above, there are workers who consider that the level of bias in index methods is unacceptably high, and that the technique is misleading and should be avoided. Others, on the other hand, although they would undoubtedly agree that the question if by no means difinitely settled are clear enough in their own minds that trap indices, properly obtained are convenient and useful data. Hansson (1967) in particular has reviewed the possible sources of differences in trappability; and although he makes some minor criticisms of Linn's proposed method, he nevertheless comes to the conclusion that the index, despite its faults, has a useful part to play in small mammal ecological investigations.

It is not proposed here to enter into a discussion of the merits and demerits of various methods which have been proposed for the collection of index data. Linn (1954, 1963), Southern \& Linn (1964) and Souther n (1965) have suggested trap lines, but a grid is also possible as used by Southern (1973) and many others. The precise way in which the line or grid is set is critical in obtaining minimum bias of trappability Linn and his students have devoted some time to attempting to define and analyse the nature and causation of variation in trappability, and have come to the conclusion that a great deal can be done to minimise trapping bias, and to approximate to the ideal of uniform trappability on which the mathematics which follows (and practically all other mathematics used for the analysis of trapping data) is based. The observations and arguments regarding trappability variation, and the means of minimising it, will be published elsewhere. Meanwhile, the authors consider that it is worth while to continue with a discussion of the methods of analysis of trap index data, once they have been collected.

The trapping index method has, in the past, suffered from the difficulty that no simple statistical test had been developed which could be used to estimate the significance of differences in paired data. It was, therefore difficult to be sure how different the total catches in two samples had to be before the difference could be regarded as significant; and similarly for comparison of single species catches in two multi-species samples,
or for the catches of two species within a single sample. Consequently, in the past simple comparisons of this sort have been avoided, and trapping index data used only in groups, to demonstrate some broad general trend. Linn (1954) shows this approach clearly. Nevertheless, there are many cases in which it would be valuable to be able to make simple, direct comparisons of paired data. The purpose of this paper is to present a fairly straightforward mathematical technique for this purpose.

## 2. METHODS OF ANALYSING INDEX TRAPPING DATA

It is necessary to emphasise at the outset that the technique to be described involes comparison of capture rates. When a number of traps are used in the field to catch small mammals of a variety of species, the numbers caught of the different species provide no direct information about the numbers of these species living in the area where the traps were set. The data provide information only about the relative capture rates of the different species. It is only when the critical assumption is made, that these capture rates are proportional to population numbers, that a comparison of two capture rates is equivalent to a comparison of two population sizes. This is an assumption which, as has been implied above, must not be made lightly. Only when every possible precaution has been taken to ensure that the inevitable variations in trappability are kept to an absolute minimum can meaningful comparisons be made.

## 3. METHODS OF COMPARING CAPTURE RATES

It is supposed that the traps are set out for a unit time (which is chosen for convenience but in practice is 24 hours or some multiple thereof; but see later) and that the capture rate relative to this unit time for the $i$ th species $(i=1,2, \ldots, s)$ is $\lambda_{i}$. That is, for a single trap in an area containing only the $i$ th species, the probability that an animal is caught during a short interval of time $\delta t$ (assuming the trap is not already occupied) is $\lambda_{i} \delta t+o(\delta t)$.

Thus for a single trap placed for unit time in an area containing a species, an animal of the $i$ th species is caught provided it is caught before any animal of the other species. On the assumptions above this probability is given by

$$
\begin{equation*}
\int_{0}^{1} \lambda_{i} e^{-\lambda_{i} t} e^{-t \sum_{j \neq i} \lambda_{j}} d t=\lambda_{j}\left(1-e^{-i}\right) / \lambda \tag{1}
\end{equation*}
$$

where

$$
\lambda=\sum_{j=1}^{s} \lambda_{j} .
$$

In addition, the probability that during the unit time no animal of any species is caught is given by $e^{-\lambda}$.
Consider now a total of $t$ traps, of which $a_{o}$ are found to contain no animals and $a_{1}, a_{2}, \ldots, a_{s}$ are found to contain animals of species 1,2 , $\ldots, s$, respectively, and $\sum_{r=0}^{s} a_{r}=t$. Then the likelihood of these particular results is proportional to

$$
\begin{equation*}
e^{-a_{o} \lambda}\left(1-e^{-\lambda}\right) t-a_{o}\left\{{\underset{i=1}{s} \lambda_{\mathrm{i}}}^{a_{i}}\right\} \mid \lambda^{t-a_{n}} \tag{2}
\end{equation*}
$$

The method of Maximum Likelihood (see, for example, Kendall \& Stuart (1961) pp. 51 et seq.), may now be used to obtain estimates of the capture rates $\lambda_{i}$ and approximate values of the standard errors of these estimates.
From (2), the equations for these estimates are, for $i=1,2, \ldots, s$,

$$
\begin{equation*}
\frac{\partial \log L}{\partial \lambda_{\mathrm{i}}}=-t+\frac{t-a_{0}}{1-e^{-\lambda}}-\frac{t-a_{0}}{\lambda}+\frac{a_{i}}{\lambda_{i}}=0 \tag{3}
\end{equation*}
$$

These equations may readily be solved, provided $a_{0} \neq 0$, to give

$$
\begin{equation*}
\hat{\lambda}_{i}=-\frac{a_{i}}{t-a_{0}} \log \frac{a_{0}}{t}, i=1,2, \ldots, s \tag{4}
\end{equation*}
$$

Then in the usual way the asymptotic variances and covariances of these estimates are given by the inverse of the matrix whose elements are $E\left\{\partial{ }^{2} \log L / \partial \lambda_{i} \partial \lambda_{j}\right\}$. The general expressions derived in this way are extremely complicated and only a few special cases of practical importance will be considered.
(1) Where only one species is caught $(s=1)$, or alternatively where all the species are included together for the purpose of estimating the overall capture rate, we obtain from (4) this estimate to be

$$
\begin{equation*}
\hat{\lambda}=-\log -\frac{a_{0}}{t} \tag{5}
\end{equation*}
$$

It may be noted that because of the additivity of the capture rates this result may be obtained either by considering $s=1$, in which case $a_{0}+a_{1}=$ $t$ in (4), or by letting $\hat{\lambda}=\sum_{i=1}^{s} \hat{\lambda}_{i}$, for the case where the $s$ species are taken together.
Also

$$
\begin{equation*}
\left.E\left\{\partial^{2} \log L / \partial \lambda^{2}\right\}=-E\left\{\left(t-a_{0}\right) e^{-\lambda} /\left(1-e^{-\lambda}\right)^{2}\right\}=-t e^{-\lambda} / 1-e^{-\lambda}\right) \tag{6}
\end{equation*}
$$

since

$$
E\left(a_{0}\right)=e^{-\lambda} t .
$$

The variance of $\lambda$ is, asymptotically, given by

$$
\left(1-e^{-\lambda}\right) / t e^{-\lambda}
$$

and hence by substituting $\hat{\lambda}$ for $\lambda$ the estimate of the standard error of $\hat{\lambda}$ is given by

$$
\begin{equation*}
\nu\left\{\left(t-a_{0}\right) / a_{0} t\right\}=\nu\left\{\frac{1}{a_{0}}-\frac{1}{t_{0}}\right\} \tag{7}
\end{equation*}
$$

Thus for comparing the capture rates for two different samples, supposing that $t_{1}$ traps resulted in $a_{10}$ empty traps in the first sample and $t_{2}$ traps resulted in $a_{20}$ empty traps in the second sample, we have estimates of the capture rates of $\hat{\lambda}_{1}$ and $\hat{\lambda}_{2}$ for the two samples, respectively, where

$$
\hat{\lambda}_{1}=-\log \frac{a_{10}}{t_{1}} \quad \text { and } \quad \hat{\lambda}_{2}=-\log \frac{a_{20}}{t_{2}}
$$

and the estimated standard error of

$$
\begin{equation*}
\hat{\lambda}_{1}-\hat{\lambda}_{2}=\log \left(t_{1} a_{20} / t_{2} a_{10}\right) \tag{8}
\end{equation*}
$$

is given by

$$
\begin{equation*}
v\left\{\frac{1}{a_{10}}+\frac{1}{a_{20}}-\frac{1}{t_{1}}-\frac{1}{t_{2}}\right\} \tag{9}
\end{equation*}
$$

If the ratio of expression (8) to expression (9) exceeds 2 in numerical value ( 2 being a sufficiently close approximation in this context to 1.96 , the 5 per cent point of the normal distribution) the capture rates (and hence the population sizes, if the proportionality holds) for the two samples are significantly different at the 5 per cent level.
(2) The case of two species $(s=2)$ covers the cases where either there are actually only two species present, or where alternatively only one of many species is of interest and those species which are not of interest are combined together for the purpose of analysis.

In this case there are, for each sample, two capture rates $\lambda_{1}$ and $\lambda_{2}$ with estimates

$$
\begin{equation*}
\hat{\lambda}_{i}=-\frac{a_{i}}{t-a_{0}} \log \frac{a_{0}}{t}, \quad i=1,2 \tag{10}
\end{equation*}
$$

The variances and covariance of these estimates are given by

$$
\begin{equation*}
\operatorname{var}\left(\lambda_{i}\right) \approx \frac{\lambda_{1} \lambda_{2}}{t\left(1-e^{-\lambda}\right)}+\frac{\lambda_{i}^{2}\left(1-e^{-\lambda}\right)}{t \lambda^{2} e^{-\lambda}}, \quad i=1,2 \tag{11}
\end{equation*}
$$

and

$$
\begin{equation*}
\operatorname{cov}\left(\lambda_{i}, \lambda_{j}\right) \approx-\frac{\lambda_{1} \lambda_{2}}{t\left(1-e^{-\lambda}\right)}+\frac{\lambda_{1} \lambda_{2}\left(1-e^{-\lambda}\right)}{t \lambda^{2} e^{-\lambda}} \tag{12}
\end{equation*}
$$

The estimated standard error of $\hat{\lambda}_{1}$ is given by

$$
\begin{equation*}
\vee\left\{\frac{a_{1} a_{2}\left[\log \left(a_{0} / t\right)\right]^{2}}{\left(t-a_{0}\right)^{3}}+\frac{a_{i}{ }^{2}}{a_{0} t\left(t-a_{0}\right)}\right\} \tag{13}
\end{equation*}
$$

It should be remembered that in these formulae $\lambda=\lambda_{1}+\lambda_{2}$ and $t=a_{0}+$ $a_{1}+a_{2}$.

For data obtained as follows:

|  | Empty | Species 1 | Species 2 | Total |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Sample | 1 | $a_{10}$ | $a_{11}$ | $a_{12}$ | $t_{1}$ |
|  | 2 | $a_{20}$ | $a_{21}$ | $a_{22}$ | $t_{2}$ |

two types of pairwise comparison are possible. These are either the comparison of a single species between samples e.g. comparing $\lambda_{11}$, the capture rate for species 1 in sample 1 , with $\lambda_{21}$, the capture rate for species 1 in sample 2 or alternatively the comparison of two species within a single sample e.g. comparing $\hat{\lambda}_{11}$ with $\hat{\lambda}_{12}$. This last comparison can only be made using this particular analysis, if there are only two species with all the other species taken together in the sample. The case of within sample comparison, when more than two species is present, is dealt with later.
(a) Comparison between Samples

The estimate of the difference between capture rates for species 1 (and similarly for species 2) is

$$
\begin{equation*}
\hat{\lambda}_{11}-\hat{\lambda}_{21}=\frac{a_{21}}{t_{2}-a_{20}} \log \frac{a_{20}}{t_{2}}-\frac{a_{11}}{t_{1}-a_{10}} \log \frac{a_{10}}{t_{1}} \tag{14}
\end{equation*}
$$

This has estimated standard error

$$
\begin{gather*}
\vee \frac{a_{11} a_{12} \mid \log \left(a_{10} / t_{1}\right) i^{2}}{\left(t_{1}-a_{10}\right)^{3}}+\frac{a_{21} a_{22}\left|\log \left(a_{20} / t_{2}\right)\right|^{2}}{\left(t_{2}-a_{20}\right)^{3}}+ \\
\left.+\frac{a^{2}{ }_{11}}{a_{10} t_{1}\left(t_{1}-a_{10}\right)}+\frac{a^{2}{ }_{21}}{a_{20} t_{2}\left(t_{2}-a_{20}\right)}\right\} \tag{15}
\end{gather*}
$$

For an approximate 5 per cent significance test the two standard error rule may again be used.
(b) Comparison within Samples

The estimate of the difference between capture rates for the two species in sample 1 is

$$
\begin{equation*}
\hat{\lambda}_{11}-\hat{\lambda}_{12}=\frac{a_{12}-a_{11}}{t_{1}-a_{10}} \log \frac{a_{10}}{t_{1}} \tag{16}
\end{equation*}
$$

Because these estimates are correlated the estimated standard error of (16) is given, not by an expression similar to (15), but by

$$
\begin{equation*}
\nu\left\{\frac{4 a_{11} a_{12}\left|\log \left(a_{10} / t_{1}\right)\right|^{2}}{\left(t_{1}-a_{10}\right)^{3}}+\frac{\left(a_{11}-a_{12}\right)^{2}}{a_{10} t_{1}\left(t_{1}-a_{10}\right)}\right\} \tag{17}
\end{equation*}
$$

(3) Where it is required to compare two species within a single sample $(s=3)$, it is sufficient to consider the case of three species only, the third species being made up of all those species other than those of immediate interest.

For a single sample the estimates of the three capture rates are given by

$$
\begin{equation*}
\hat{\lambda}_{\mathrm{i}}=-\frac{a_{i}}{t-a_{0}} \log \frac{a_{0}}{t}, \quad i=1,2,3 \tag{18}
\end{equation*}
$$

and the variances and covariances of these estimates are given by

$$
\begin{equation*}
\operatorname{var}\left(\hat{\lambda_{i}}\right) \approx \frac{\lambda \lambda_{i}}{t\left(1-e^{-\lambda}\right)}-\frac{\lambda^{2} i}{t}\left\{\frac{1}{1-e^{-\lambda}}-\frac{1-e^{-\lambda}}{\lambda^{2} e^{-\lambda}}\right\}, \quad i=1,2,3 \tag{19}
\end{equation*}
$$

and

$$
\begin{equation*}
\operatorname{cov}\left(\hat{\lambda}_{i}, \hat{\lambda}_{j}\right) \approx-\frac{\lambda_{i} \lambda_{j}}{t}\left\{\frac{1}{1-e^{-\lambda}}-\frac{1-e^{-\lambda}}{\lambda^{2} e^{-\lambda}}\right\} \tag{20}
\end{equation*}
$$

Notice that (19) reduces to (11) if one of the $\lambda_{i}$ 's is zero, and that (20) is identical with (12).

From (19) and (20) the variance of $\hat{\lambda}_{j}-\hat{\lambda}_{j}$ is given by

$$
\begin{equation*}
\operatorname{var}\left(\hat{\lambda}_{i}-\hat{\lambda}_{j}\right) \approx \frac{\lambda\left(\lambda_{i}+\lambda_{j}\right)}{t\left(1-e^{-\lambda}\right)}-\frac{\left(\lambda_{i}-\lambda_{j}\right)^{2}}{t}\left\{\frac{1}{1-e^{-\lambda}}-\frac{1-e^{-\lambda}}{\lambda^{2} e^{-\lambda}}\right\} \tag{21}
\end{equation*}
$$

The estimated standard error of $\lambda_{i}$ is therefore given by

$$
\begin{equation*}
\nu\left\{\frac{a_{i}\left[\log \left(a_{0} / t\right)\right]^{2}\left(t-a_{0}-a_{i}\right)}{\left(t-a_{0}\right)^{3}}+\frac{\mathrm{a}^{2}{ }_{\mathrm{i}}}{a_{0} t\left(t-a_{0}\right)}\right\} \tag{22}
\end{equation*}
$$

while the estimated standard error of $\lambda_{i}-\lambda_{j}$ is given by

$$
\begin{equation*}
\vee\left\{\frac{\left[4 a_{i} a_{j}+a_{k}\left(a_{i}+a_{j}\right)\right]\left[\log \left(a_{0} / t\right)\right]^{2}}{\left(t-a_{0}\right)^{3}}+\frac{\left(a_{i}-a_{j}\right)^{2}}{a_{0} t\left(t-a_{0}\right)}\right\} \tag{23}
\end{equation*}
$$

where $a_{k}$ denotes the number of the third species caught. If $a_{k}=0$ this reduces, as it should, to an expression equivalent to the standard error given by (17).

Three general points may also be made. It has been assumed that for different samples the traps were laid down for the same length of time.
, If this is not the case modifications by suitable scaling factors will need to be made to the above formulae. In addition it has been assumed that $a_{0} \neq 0$, that is, that some empty traps remained. If this is not the case the above formulation is not valid, and in general if $a_{0}=0$ comparison between samples will not be possible. Finally, natural logarithms (to base e) have been used throughout. If it is required to employ tables of logarithms to base 10 the conversion $\log _{e} x=2.302585 \log _{10} x$ should be used.

## 4. SOME SPECIFIC EXAMPLES

To help the ecologist to thread his way through the foregoing, and to use the method, some practical examples follow. Consider the following data:

|  |  | Empty | Species 1 | Species 2 | Species 3 | Total |
| :--- | :--- | :---: | :---: | :---: | :---: | :---: |
| Sample 1 | $6\left(a_{10}\right)$ | $13\left(a_{11}\right)$ | $25\left(a_{12}\right)$ | $6\left(a_{18}\right)$ | $50\left(t_{1}\right)$ |  |
| Sample 2 | $18\left(a_{20}\right)$ | $10\left(a_{21}\right)$ | $7\left(a_{22}\right)$ | $15\left(a_{23}\right)$ | $50\left(t_{2}\right)$ |  |

The estimates of the overall capture rates are given by

$$
\hat{\lambda}_{1}==\log \left(a_{10} / t_{1}\right)=2.1202 ; \hat{\lambda}_{2}=-\log \left(a_{20} / t_{2}\right)=1.0217
$$

The estimates of the individual capture rates (from equation (4)) are as follows:

|  | Species 1 | Species 2 | Species 3 | Total |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Sample 1 | $0.6264\left(\hat{\lambda}_{11}\right)$ | $1.2047\left(\hat{\lambda}_{12}\right)$ | $0.2891\left(\hat{\lambda}_{13}\right)$ | $2.1202\left(\hat{\lambda}_{1}\right)$ |
| Sample 2 | $0.3193\left(\hat{\lambda}_{21}\right)$ | $0.2235\left(\hat{\lambda}_{22}\right)$ | $0.4789\left(\hat{\lambda}_{23}\right)$ | $1.0217\left(\hat{\lambda}_{2}\right)$ |

Note the additive nature of the individual capture rates.
(1) Differences between Overall Capture Rates of Samples

The difference between the estimated overall capture rates for the two samples is

$$
\hat{\lambda}_{1}-\hat{\lambda}_{2}=1.0985
$$

The estimated standard error of this difference (from equation (9)) is $\nu 0.1822=0.4268$.

Since $1.0985 / 0.4268=2.57$, there is evidence of a significant difference in capture rates, because this ratio is greater than 2.
[It may be noted that the simple test for difference of proportions in empty traps gives $p_{1}-p_{2}=-0.24$ with standard error of 0.0828 resulting a ratio of -2.90 . This is roughly comparable with the value of 2.57 above (the difference in sign being
ignored), although the difference between them emphasises the fact that both techniques are approximate cnly. It suggests that the technique based on capture rates may be somewhat conservative in detecting significant differences.]
(2) Comparison between Samples for Single Species

The estimated difference between the capture rates of species 1 for the two samples is

$$
\hat{\lambda}_{11}-\hat{\lambda}_{21}=0.6264-0.3193=0.3071
$$

The estimated standard error of this difference (from equation (15)) is $\nu 0.04455=0.2111$.

Note in using equation (15) that it is based on a two-species system, in which the second species is either a single species, or all species other than the first species lumped together. Thus $a_{12}$ in equation (15) is not equivalent to $a_{12}$ in the example table, but is $a_{12}+a_{13}$ (and in a general case would be $a_{12}+a_{13}+a_{14}+\ldots \ldots+a_{15}$ ). Similarly $a_{22}$ in equation (15) is $a_{22}+a_{32}$ from the example.

The ratio of the estimated difference with its standard error is $0.3071 / 0.2111=1.45$, indicating no significant difference.
(3) Comparison between Species within Samples

The estimated difference between the capture rates of species 2 and 3 within sample 1 is

$$
\hat{\lambda}_{12}-\hat{\lambda}_{13}=1.2047-0.2891=0.9156
$$

The estimated standard error of this difference (from equation (23)) is $v 0.08044=0.2836$ giving a ratio of 3.23 , which is very significant.

On the other hand, for species 2 and 3 in sample $2 \hat{\lambda}_{22}-\hat{\lambda}_{23}=-0.2554$ with standard error 0.1504 , yielding a ratio of -1.70 , which is not significant.

If seems likely that with samples of size 50 , fairly substantial differences in catch sizes will be needed to detect differences between species within samples.

When using equation (23), note that only three parameters are required. Thus $a_{i}$ and $a_{j}$ are the two species being compared, while $a_{k}$ is either the third species (as in the example) or in the general situation would be the sum of the values for all species other than the pair being compared.

## 5. SOME PRACTICAL POINTS

1. Time of trapping. It has been pointed out earlier that any convenient trapping period is permissible. In practice, the period cannot be much less than 24 hours, to allow all animals in the vicinity of the
traps to have an adequate amount of activity, and so to be at reasonable risk of capture. When the population density is high, a 24-hour trapping period will yield a reasonably high capture, and this is the ideal situation. When populations are low, it may be necessary, in order to get sample values with a reasonable chance of yielding significant differences, to trap for more than 24 hours. This raises problems because, although the trapping may go on for several days, the traps must be visisted every 24 hours at least, and the occupants released, in order to prevent trap deaths. The released animals should be marked, and if subsequently caught, the marked animals should be ignored, and the number of traps containing marked animals deducted from that day's total of traps used. For a single species situation, typical trapping data might be:

|  | Day 1 |  | Day 2 |  |  | Day 3 |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Traps used | Animals caught | Traps used | New animals caught | Marked animals caught | Traps used | New animals caught | Marked caught animals |
| Line 1 | 50 | 12 | 50 | 3 | 6 | 50 | 1 | 7 |
| Line 5 | 50 | 18 | 50 | 10 | 10 | 50 | 5 | 16 |

Data for analysis would then be:

$$
\left.\begin{array}{c}
\text { Line } 1 \quad a_{10}=(50-12)+(50-9)+(50-8)=121 \quad a_{11}=12+3+1=16 \\
t_{1}=50+(50-6)+(50-7)=137 \\
\text { Line } 2
\end{array} a_{20}=(50-18)+(50-20)+(50-21)=91 \quad a_{21}=18+10+5=33\right)=124 .
$$

These calculations ignore the potential information about absolute population size, which is contained in the numbers of marked animals recaptured. One of the various capture-recapture methods of analysis (see, for example, Southwood, 1966; p. 75 et seq.) might possibly be used in this case, but additional assumptions, which would need careful examination, would be required about the trappability of previously caught animals. It should also be noted, perhaps, that it might be possible to analyse the above data using one of the variants of the so-called »removal« method (Southwood, 1966; p. 181 et seq.), although the animals, after first capture, are marked, returned to the population, and subsequently ignored, rather than being physically removed. This procedure has the advantage of keeping to a minimum the artificial stimulus to immigration, which is an undesirable result of removal of part of a population. There is also the advantage that, if the data are analysed as suggested by Ryszkowski (1969), the assumption of equal trappability throughout the trapping period is not required. However, it would be necessary to consider cerefully whether the rather small amount of sampling effort for which the method described in this paper is designed would provide enough information for a satisfactory »removal« analysis.

One further point should be noted, that it is much simpler to keep the trapping period standard. It is possible to compare samples with different trapping periods, but if this is done it becomes necessary, as mentioned earlier, to apply appropriate scaling factors to the formulae.
2. Number of traps. While the methods described in this paper permit samples to be compared which have been taken with different numbers of traps, it would seem sensible to avoid comparing samples obtained by grossly different trapping efforts, for two reasons. First, since the area from which trapped animals is drawn is much larger than the dimensions of the trapping area, especially if a trap line is used, and since it is safest to assume that there is not exact proportionality between the number of traps used, and the area from which trapped animals are drawn, it would seem sensible to avoid this possible source of bias. Second, since the British environment tends to be considerably dissected, there would be obvious difficulties in attempting to compare a small sample obtained within a single habitat, against a sample obtained with a very large trapping effort which might well have crossed two or more habitats.

A further point to note is that any traps which are found to be sprung but empty must be assumed to have been out of action for the major part of the trapping period, and so must be deducted from $t$. In other words, the category of »traps empty« must be interpreted to mean »traps which, despite their having been available throughout the trapping period, have caught nothing«.
3. Number of traps empty. As has been pointed out earlier, comparisons are not possible when no traps are empty ( $a_{0}=0$ ). In practice, however, this should not be a problem, as the trapping technique must be adjusted so that there is always a reasonable proportion of empty traps. Since a trap normally catches only one animal, the situation in which all traps are full $\left(a_{0}=0\right)$ has little information value. Moreover, the reliability of an estimate falls off sharply as the $a_{0}=0$ situation is approached. The actual value of the reliability (variance of estimate of $\lambda$ divided by $\lambda^{2}$ ) of a single estimate based on a proportion $p$ of empty traps is proportional to $p\left(\log _{e} p\right)^{2 /(1-p)}$. For the relevant values of $p$ this gives:

| $p$ | $p\left(\log _{e} \mathrm{p}\right)^{2} /(1-p)$ | $p$ | $p\left(\log _{e} \mathrm{p}\right)^{2} /(1-p)$ |
| :--- | :---: | :---: | :---: |
| 0 | 0 | 0.2 | 0.6476 |
| 0.02 | 0.3123 | 0.3 | 0.6212 |
| 0.04 | 0.4317 | 0.4 | 0.5597 |
| 0.06 | 0.5052 | 0.5 | 0.4805 |
| 0.08 | 0.5547 | 0.6 | 0.3914 |
| 0.10 | 0.5891 | 0.7 | 0.2968 |

Clearly the maximum efficiency occurs close to $20 \%$ of traps empty, and for best results the operator should aim to have between $5 \%$ and $55 \%$ of this traps, empty. As a working rule $30 \%$ empty traps would seem to be a sensible objective to aim at. With the technique thus adjusted, by providing an adequately high trap density on the ground, the problem of zero empty traps should seldom if ever arise. This question of efficiency was discussed in a different, but analogous, context by Fisher (1960, p. 222), who suggested somewhat narrower limits for these percentages than seem appropriate in small mammal trapping investigations.
It should be mentioned that, if the situation arose in which it was essential to compare two species within a sample, with no empty traps, this can be done, but of course the comparison is less efficient, as the amount of information available is less. If $a_{1}$ traps contain species 1 and $a_{2}$ traps contain species 2 , and the capture rates are $\lambda_{1}$ and $\lambda_{2}$ respectively, then information is only available about the ratio $\lambda_{1} / \lambda_{2}$. The estimate of $\lambda_{1} / \lambda_{2}$ is $a_{1} / a_{2}$ with standard error $\nu\left\{\frac{a_{1}\left(a_{1}+a_{2}\right)}{a^{3}}\right\}$.
4. Zero captures. Zero captures present no very serious problem. Zero catch rate with zero standard error is a reasonable approximation to the true situation, given the overall imprecisions in the method. The only point to watch is, when writing computer programs, to avoid asking the machine to divide by zero.
5. Computer program. Mr. R. Discombe has written a Fortran program to enable the analyses described in this paper to be carried out on the Exeter University ICL System 4-50 computer. Details may be obtained from the Department of Biological Sciences, University of Exeter.
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## OPRACOWYWANIE DANYCH UZYSKANYCH PRZY ODEOWACH DROBNYCH SSAKOW

## Streszczenie

Rozważono użyteczność wskaźnikowej metody odłowu dla oznaczenia zagęszczenia populacji. Jakkolwiek metoda ta jest w literaturze oceniana krytycznie, to jednak można jej używać do określonych celów. Jedną z jej wad był brak prostego sposobu porównywania dwóch wskaźników i oceny zróżnicowania pomiędzy nimi.

Niniejsza sraca podaje matematyczny sposób, który umożliwia porównywanie istotności różnic np. wielkości złowień całkowitych, liczebności danego gatunku w różnych próbach, liczebności dwóch gatunków w jednej próbie. Dokonano analizy pewnych przykładów a także zwrócono uwage na ważność sposobów zbierania potrzebnych danych.

