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A Simulation Experiment on the Application of the Jackknife with Jolly's Method for the Analysis of Capture-Recapture Data

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Simulation studies have indicated that standard error formulae for estimates calculated from capture-recapture data are not reliable in practice, particularly when it comes to using them for deriving confidence limits for true population parameter values. It is therefore worth investigating alternative ways for obtaining confidence limits. One possibility is Tukey's jackknife method and in this note an experiment is described where this involved using the jackknife in conjunction with Jolly's equations for analysing capture-recapture data. It appears that a modified version of the jackknife is capable of producing valid confidence intervals and should therefore be of some value to ecologists.

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1. INTRODUCTION

If a series of samples are taken from an animal population over a period of time, with captured animals being marked and released, then a record can be kept of the captures and recaptures of all the individuals that are captured at least once. This capture-recapture data can then be used to estimate various parameters of the sampled population. A number of methods are available for the calculation of the estimates and in many cases formulae are available for standard errors. Unfortunately, however, simulation studies have indicated that the standard error formulae are not a great deal of use in practice and, in particular, these formulae cannot be relied upon for the production of valid confidence intervals for true population parameter values (M a n l y, 1971; R o f f, 1973).

In view of the doubtful value of conventional methods for calculating standard errors it was decided to investigate the use of T u k e y' s (1958) jackknife technique with capture-recapture data. When Tukey proposed this technique he conjectured that it would be useful for establishing approximate confidence intervals for a wide range of situations and since

1958 this has been confirmed by numerous theoretical and numerical studies (Gray & Shucany, 1972; Miller, 1974; Bissell & Ferguson, 1975). The results discussed in the present note suggest that the usefulness of the jackknife extends to capture-recapture data.

Eventually it is intended to study the use of the jackknife in conjunction with a number of methods for analysing capture-recapture data. This note reports the results of a first experiment in this direction, involving using the jackknife together with Jolly's (1965) equations for estimation.

2. THE JACKKNIFE

The jackknife involves dividing sample data into n comparable sized subsamples, at random if necessary. The first subsample is then removed and an unknown parameter of interest, Θ say, is estimated using the remaining data. This provides the first »partial estimate«, $\hat{\Theta}_{-1}$. The first subsample is then replaced, the second subsample is removed, and the second partial estimate, $\hat{\Theta}_{-2}$, is calculated. This process is continued until all the partial estimates $\hat{\Theta}_{-1}$, $\hat{\Theta}_{-2}$, ..., $\hat{\Theta}_{-n}$ have been obtained. These partial estimates are then combined with the estimate Θ that is obtained using the full set of data to form the »pseudo-values«

$$G_i(\hat{\Theta}) = (\hat{\Theta} - R\hat{\Theta}_{-i})/(1-R), \quad i=1,\ 2,\ ...,\ n. \tag{1}$$

The average of the pseudo-values is the jackknife estimator of Θ : —

$$G(\hat{\Theta}) = \Sigma G_i(\hat{\Theta})/n. \tag{2}$$

The properties of the jackknife estimator clearly depend upon the value of R in equation (1). When Tukey (1958) proposed the jackknife technique he used $R=(n-1)/n$, in which case the pseudo-values are simply

$$J_i(\hat{\Theta}) = n\hat{\Theta} - (n-1)\,\hat{\Theta}_{-i} \tag{3}$$

with mean

$$J(\hat{\Theta}) = \sum_{i=1}^{n} J_i(\hat{\Theta})/n \tag{4}$$

and estimated variance

$$S_J^2 = \frac{1}{n-1}\,\Sigma\{J_i(\hat{\Theta}) - J(\hat{\Theta})\}^2. \tag{5}$$

Tukey showed that this jackknife estimator will often have less bias than the usual estimator $\hat{\Theta}$ and he conjectured that the statistic

$$H_J = \{J(\Theta) - \Theta\}/\{S_J/\sqrt{n}\} \tag{6}$$

will often approximately follow a t-distribution with $n-1$ degrees of freedom. On this basis Tukey proposed confidence limits for the true value of Θ of the form

$$J(\hat{\Theta}) \pm k\, S_J / \sqrt{n} \tag{7}$$

where k is the appropriate percentage point of the t distribution.

A generalization of Tukey's jackknife that is discussed by Gray & Schucany (1972) involves allowing the R value of equation (1) to be any positive value and they showed that the statistic

$$H_G = \{G(\hat{\Theta}) - \Theta\} / \{S_J / \sqrt{n}\} \tag{8}$$

can be expected to approximately follow a t distribution with $n-1$ degrees of freedom providing that certain fairly general conditions are met (Gray & Schucany, 1972, p. 154). In particular they investigated the use of an R value of the form $(n-1)^p / n^p$, where p is positive, and showed that this will remove bias of order n^{-p} from the estimator Θ. For the experiment described in this note three forms of the jackknife were used. These were Tukey's jackknife (equation (4)), the jackknife with $R = (n-1)^2 / n^2$, and the jackknife with $R = 0$. For the third of these the jackknife estimates are simply the usual estimates $\hat{\Theta}$. It is not difficult to show that the second type of jackknife produces estimates almost exactly midway between $J(\hat{\Theta})$ and $\hat{\Theta}$.

The capture-recapture data for Jolly's (1965) estimators consists of a list of the captures and recaptures of a number of individual animals. The n subsamples needed for jackknife estimation can therefore be obtained by assigning each capture or recapture to one of the subsamples using a random process that gives each subsample the same chance of being chosen. Random numbers are convenient for this purpose. Then any one of the subsamples could have cccurred by sampling the animal population with $1/n$th of the sampling intensity that was actually used.

3. THE EXPERIMENT

A $3 \times 2 \times 2 \times 2 \times 5$ factorial design was used for the simulation experiment on the application of the jackknife. The five factors involved were as follows:

N: Population size at three levels (approximately 50, 200 and 1000 »animals«).

S: Daily survival probability at two levels (0.5 and 0.9).

P: Sampling intensity at two levels (low and high, as discussed below).

G: Two populations were generated for five »days« each, for each combination of the factor levels N, S and P.

R: Each population was independently samples five times where each sampling involved taking one sample per »day« for the five »days« that the population was generated.

Thus 120 sets of capture-recapture data were obtained with each set covering a five »day« period. Details of the methods of simulation will be found elsewhere (Manly, 1970, 1971). High and low sampling intensities were achieved by varying the probability of capturing »animals« in samples. It was necessary to treat the three population sizes differently in this respect and the probabilities of capture shown in the following table were applied.

Probabilities of Capture

Population size (approx)	Sampling Intensity	
	Low	High
50	0.5	0.75
200	0.2	0.6
1000	0.1	0.3

Each set of capture-recapture data was used to estimate the population size on day 3 (N_3), the proportion of animals surviving from day 2 to day 3 (Φ_2), the number of animals entering the population during day 2 (B_2), and also $\log(N_3)$ and $\log(\Phi_2)$. Jolly's (1965) equations with the bias corrections suggested by Seber (1973, p. 204) were the basis for estimation. The logarithmic transformations of N_3 and Φ_2 were tried because pilot simulations indicated that these transformations would be useful for jackknife estimates. Since estimates of B_2 were sometimes negative the logarithmic transformation could not be used with this parameter.

Jackknife estimates were calculated using R values of $(n-1)/n$, $(n-1)^2/n^2$, and 0. In all cases 30 subsamples were used. The estimates were converted to H values using equation (8) since the usefulness of jackknifing in dependent upon the distribution of these H values. In the next section of this note H_J will denote the H value for the jackknife with $R=(n-1)/n$ (*i.e.* Tukey's jackknife), H_2 will denote the H value for the jackknife with $R=(n-1)^2/n^2$, and H_0 will denote the H value for the jackknife with $R=0$ (where the jackknife estimate is the conventional estimate).

The jackknife method failed completed for two of the 120 data sets because the Z values for Jolly's (1965) equations were zero. However it seems fair to regard this as primarily a failure of Jolly's equations since when this occurs the estimate of population size is simply the number of animals captured. At any rate the two data sets involved were not included for the analysis of results as described in the next section.

4. RESULTS

Analysis of Variance (ANOVA) was used to analyse the distributions that were obtained for H values and a summary of result is shown in Table 1. With 30 subsamples standard jackknife theory suggests that the H values might approximately follow standard normal distributions but this is clearly not true since all of the variances are much smaller than unity and many of the means are significantly different from zero. This is disappointing but the situation is not as bad as it might have been since the ANOVA's do at least indicate that the means of the H-values are on the whole not strongly affected by the factors that

Table 1

Summary of analyses of variance on the H_J, H_2 and H_0 values obtained from the sampling experiment.

Estimation of	Statistic	Overall mean	Overall variance (117 df)	Factors and or interactions that have a significant effect on the mean
	H_J	−0.28***	0.610	NP (5% level)
N_3	H_2	−0.28***	0.510	None
	H_0	−0.29***	0.439	None
	H_J	0.04	0.524	None
log (N_3)	H_2	−0.08	0.365	None
	H_0	−0.17**	0.323	None
	H_J	−0.23**	0.678	None
φ_2	H_2	−0.18**	0.461	None
	H_0	−0.12*	0.380	None
	H_J	0.04	0.585	SP (5% level)
log (φ_2)	H_2	0.00	0.369	None
	H_0	−0.04	0.295	G (5% level)
	H_J	−0.17**	0.467	None
B_2	H_2	−0.13*	0.327	None
	H_0	−0.10*	0.270	None

* Significantly different from zero at the 5% level,
** Significantly different from zero at the 1% level,
*** Significantly different from zero at the 0.1% level.

were examined in the experiment. Furthermore, ANOVA's on the logarithms of variance estimates provide no evidence to suggest that variances are not constant for all combinations of factor levels. It therefore does at least appear that the distributions of the H values are stable.

It is interesting to note that the H_J values have rather larger variances than the H_2 values which in turn have somewhat larger variances than the H_0 values. Presumably the random choice of subsamples is responsible for this phenomena since it introduces a source of variation which does not affect H_0 and affects H_J more than H_2.

The variances of less than unity for the H values can be explained by a negative correlation between pseudo-values (G r a y & S c h u c a n y, 1972, p. 165) and corrections can be made to the jackknife procedures to take it into account. Thus Table 1 suggests that confidence limits for population sizes can best be obtained by assuming that the H_2 values for estimates of the logarithm of the size follow a normal distribution with mean zero and standard deviation 0.6 and on this basis the confidence limits

$$G_2(\log \hat{N}) \pm 0.6\, k\, S_J/\sqrt{n} \qquad (9)$$

can be used where $G_2(\log \hat{N})$ is the jackknife estimate with $R=(n-1)^2/n^2$ and k is the appropriate percentage point for the standard normal distribution. These confidence limits for log N can obviously be »uncoded« to give limits for the population size N. Clearly these limits will be

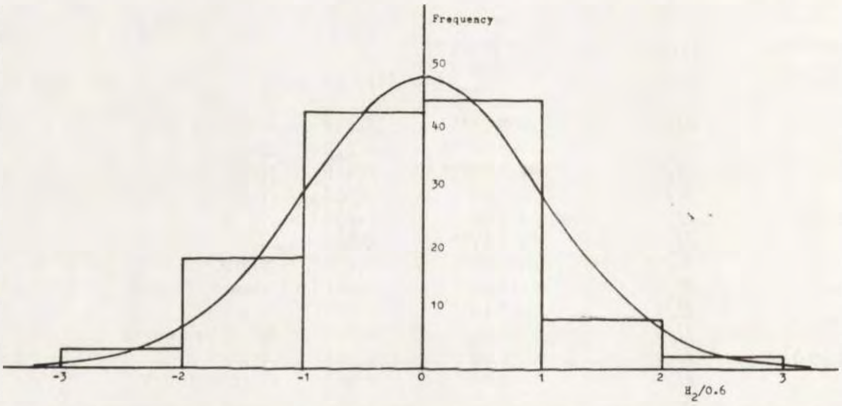

Fig. 1. The histogram shows the distribution of the values of $H_2/0.6$ for the experimental estimates of $\log(N_3)$. The smooth curve is the standard normal distribution.

realistic providing that $H_2/0.6$ approximately follows a standard normal distribution and the results of the sampling experiment suggest that this is the case, as shown by Figure 1.

Table 1 also suggests that confidence limits for log Φ (and hence Φ) are best based upon the assumption that the H_2 values for log Φ are normally distributed with mean zero and standard deviation 0.6. These confidence limits will be of the form

$$G_2(\log \hat{\Phi}) \pm 0.6\, k\, S_J/\sqrt{n} \qquad (10)$$

and they will be realistic providing that $H_2/0.6$ follows a standard normal distribution. Figure 2 shows that the experimental results support this conclusion.

Unfortunately all of the H values for B_2 estimates have means significantly different from zero. However confidence limits can be calculated to take this into account. Thus if it is assumed that H_0 is normally distributed with mean -0.1 and standard deviation 0.52 then confidence limits for a true number of births will be of the form

$$\hat{B}-0.52(k-0.1)S_J/\sqrt{n} \quad \text{and} \quad \hat{B}+0.52(k+0.1)S_J/\sqrt{n} \tag{11}$$

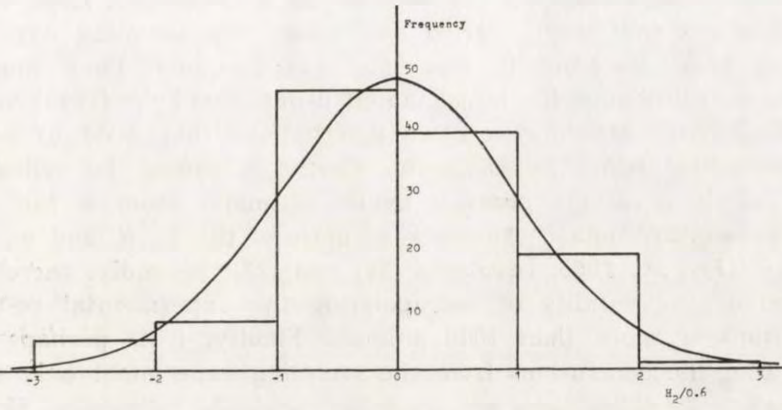

Fig. 2. The histogram shows the distribution of the values of $H_2/0.6$ for the experimental estimates of $\log(\Phi_2)$. The smooth curve is the standard normal distribution.

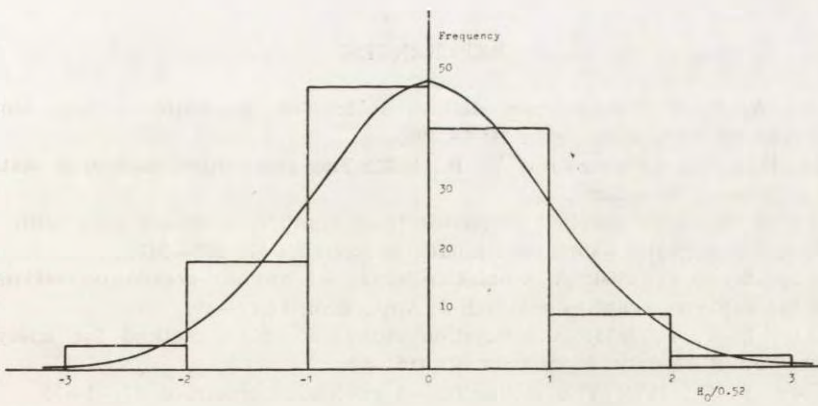

Fig. 3. The histogram shows the distribution of the values of $H_0/0.52$ for the experimental estimates of B_2. The smooth curve is the standard normal distribution.

In practice there will be little error involved in ignoring the non-zero mean of H_0 and simply using the limits

$$\hat{B} \pm 0.52\, k\, S_J/\sqrt{n} \tag{12}$$

instead. Figure 3 shows the observed distribution of values of $H_0/0.52$ for the experimental estimates of B_2 and there is a clear indication of the slightly negative mean.

5. CONCLUSIONS

The reasonableness of the confidence limits given by equation (9) to (12) is confirmed by examining the results obtained from a large number of simulations that were carried out before the sampling experiment that has been described in this note was designed. They should be superior to confidence limits calculated using Jolly's (1965) variance formulae. There are however two reservations that need to be born in mind when using the jackknife. Firstly, it cannot be relied upon when Jolly's equations produce trivial estimates from a full set of capture-recapture data because one or more of the Z_i, R_i and m_i values are zero (Jolly, 1965, equations (22) and (23). Secondly, there is the question of the validity of extrapolating the experimental results to populations of more than 1000 animals. Finally, it is perhaps worth noting that the conclusions from the sampling experiment only strictly apply when 30 subsamples are used for jackknife estimation. However some simulations that will not be reported in detail suggest that the number of subsamples used does not make a great deal of difference to the properties of jackknife estimators providing that there are more than about 20.

REFERENCES

1. Bisel A. F. & Ferguson R. A., 1975: The jackknife — toy, tool or two-edged weapon. Statistician *24*: 79—99.
2. Gray H. L. & Schucany W. R., 1972: The generalized jackknife statistic. Marcel Dekker: New York.
3. Jolly G. M., 1965: Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika *52*: 225—247.
4. Manly B. F. J., 1970: A simulation study of animal population estimation using the capture-recapture method. J. Appl. Ecol. 7: 13—39.
5. Manly B. F. J., 1971: A simulation study of Jolly's method for analysing capture-recapture data. Biometrics *27*: 415—424.
6. Miller R. G., 1974: The jackknife — a review. Biometrika *61*: 1—15.
7. Roff D. A., 1973: On the accuracy of some mark-recapture estimators. Oecologia (Berl.) *12*: 15—34.
8. Seber G. A. F., 1973: Estimation of animal abundance and related parameters. Griffin: 1—506. London.
9. Tukey J. W., 1958: Bias and confidence in not-quite large samples (Abstract). Ann. Math. Statist. 29: 614.

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SYMULACYJNY EKSPERYMENT ZASTOSOWANIA METODY „JACKKNIFE" WRAZ Z METODĄ JOLLY'EGO DO ANALIZY DANYCH UZYSKANYCH Z POWTÓRNEGO ODŁOWU

Streszczenie

Symulowane badania wykazały, że wzór na błąd standardowy estymacji danych uzyskanych metodą powtórnego odłowu nie jest w praktyce pewny, szczególnie, gdy stosuje się go do obliczania granic ufności dla wybranych parametrów populacyjnych. Celem pracy jest zatem poszukiwanie innych dróg dla uzyskania granic ufności. Jedną z możliwości jest metoda „jackknife" Tukey'a. W powyższej pracy opisano eksperyment, który dotyczy użycia metody „jackknife" w połączeniu z równaniami Jolly'go dla analizy danych, uzyskanych za pomocą powtórnego odłowu (Ryc. 1, 2, 3).

Wydaje się, że zmodyfikowana wersja metody „jackknife" jest w stanie dostarczyć prawdziwych przedziałów ufności, powinna zatem stanowić pewną wartość dla ekologów.