A Method for Population Estimation from a Single Release Experiment

Kohji YAMAMURA,¹ Sadao WAKAMURA^{2,3} and Shuji KOZAI^{2,4}

¹*Laboratory of Biometrics, National Institute of Agro-Environmental Sciences,
Tsukuba, Ibaraki 305, Japan*

²*Laboratory of Applied Entomology, Shikoku National Agricultural
Experiment Station, Zentsuji, Kagawa 765, Japan*

(Received June 11, 1990; Accepted October 29, 1991)

A simple method was considered to estimate population size from a release-recapture experiment where marked individuals are released only once and all of the captured individuals are removed from the population. This method was applied to a population estimation of *Spodoptera litura* (FABRICIUS) (Lepidoptera: Noctuidae). The estimates were compared with those obtained by the JOLLY-SEBER method which requires a multiple-release experiment. The results of our conservative estimation were similar to those obtained by the JOLLY-SEBER method, which suggested the practical usefulness of our method.

Key words: estimation, method, marking, release, recapture

INTRODUCTION

Various methods have been proposed to estimate population size from marking-recapture data (SEBER, 1982). Many of these methods are based on a process in which a part of the field population is captured, marked and subsequently returned to the field. Some commercial traps, however, kill the animals. In some cases, animals reared in a laboratory should be marked and released. SEBER (1962) proposed an applicable method for population estimation in such situations. This laborious method requires at least two releases and two sampling censuses, and that at least one release operation be conducted just after a sampling operation. PARKER (1963) considered a parsimonious method which can be applied to single-release experiments in which animals are released only once. To use his method, however, we must conduct sampling censuses at least three times, and also need some iterative calculations to obtain maximum likelihood estimates.

We therefore propose another method which can be applied to an experiment where sampling censuses are conducted only twice. This method is based on the assumption that the wild population size remains constant. Similar assumptions were used by HAMADA (1976).

³ Present address: *Laboratory of Behavior Regulation, National Institute of Sericultural and Entomological Science, Tsukuba, Ibaraki 305, Japan*

⁴ Present address: *Research Project Team, Shikoku National Agricultural Experiment Station, Zentsuji, Kagawa 765, Japan*

METHOD

We must use the following assumptions:

- (1) The wild population size is constant during two consecutive sampling censuses. Even if many wild individuals are lost by emigration from the study area or by artificial removal, the wild population size returns to the original level through immigration from the surrounding area.
- (2) The proportion of marked individuals which survive and stay in the population between the two successive censuses, i.e., the rate of remaining, is constant.
- (3) Both marked individuals and wild individuals in the population have the same probability of being captured.
- (4) Marked individuals do not lose their marks, and all marks are reported when they are recaptured.

Let

- ϕ : proportion of marked individuals which survive and stay in the population between the successive censuses,
- U : wild population size,
- M_0 : number of marked individuals released into the population (release time=0),
- M_i : number of marked individuals remaining in the population at time i ,
- N_i : total number of individuals in the population at time i ,
- u_i : number of wild individuals captured at time i ,
- m_i : number of marked individuals recaptured at time i ,
- n_i : total number of individuals captured at time i ($=m_i+u_i$).

Then, we have the following deterministic equations:

$$\begin{aligned} M_1 &= \phi M_0, \\ M_2 &= \phi (\phi M_0 - m_1), \\ N_1 &= U + \phi M_0, \\ N_2 &= U + \phi (\phi M_0 - m_1). \end{aligned}$$

If n_i is not treated as a random variable, the expectation of m_1 is:

$$E(m_1) = n_1 M_1 / N_1, \quad (1)$$

and the conditional expectation of m_2 for a given m_1 is:

$$E(m_2/m_1) = n_2 M_2 / N_2. \quad (2)$$

If the sampling fraction (n_i/N_i) is not so large, the probability distributions of m_i can be approximated by binomial distribution. Then, the joint probability function (likelihood function) is:

$$L = \binom{n_1}{m_1} \left(\frac{M_1}{N_1}\right)^{m_1} \left(\frac{U}{N_1}\right)^{u_1} \binom{n_2}{m_2} \left(\frac{M_2}{N_2}\right)^{m_2} \left(\frac{U}{N_2}\right)^{u_2}. \quad (3)$$

The maximum likelihood estimates of ϕ and U which satisfy $\partial \log L / \partial \phi = 0$ and $\partial \log L / \partial U = 0$ can be obtained by solving the equations (1) and (2) where the expectations are replaced with their observed values:

$$\hat{\phi} = \frac{u_1 m_2}{m_1 u_2} + \frac{m_1}{M_0}, \quad (4)$$

$$\hat{U} = \hat{\phi} M_0 u_1 / m_1. \quad (5)$$

The variances can be estimated approximately using the TAYLOR series expansions (SEBER, 1982):

$$\begin{aligned} \hat{V}(\hat{\phi}) = & \left\{ \frac{1}{M_0} - \frac{(m_1 + u_1) m_2}{m_1^2 u_2} \right\}^2 \hat{V}(m_1) \\ & + \left\{ \frac{u_1 (m_2 + u_2)}{m_1 u_2^2} \right\}^2 \hat{V}(m_2), \end{aligned} \quad (6)$$

$$\begin{aligned} \hat{V}(\hat{U}) = & \left\{ \frac{2 M_0 u_1 (m_1 + u_1) m_2}{m_1^3 u_2} + 1 \right\}^2 \hat{V}(m_1) \\ & + \left\{ \frac{M_0 u_1^2 (u_2 + m_2)}{m_1^2 u_2^2} \right\}^2 \hat{V}(m_2), \end{aligned} \quad (7)$$

where

$$\hat{V}(m_i) = \frac{(\hat{U} - u_i) u_i m_i}{\hat{U} (u_i + m_i)}. \quad (8)$$

APPLICATION

Marking experiments were conducted in the western district of Kagawa Prefecture, northern Shikoku, Japan in 1985 (WAKAMURA et al., 1990). Males of *Spodoptera litura* (FABRICIUS) (Lepidoptera: Noctuidae) reared in a laboratory were marked and released in the evening from the 4 release points. Males were captured with 24 water-pan type sex pheromone traps. The distances between the release points and the traps range from 0.13 to 23.20 km. The longest distance among the 4 release points was 5.3 km in our experiments. In this populations estimation, therefore, we restricted the study area within the 6 km diameter circle including the 4 release points. u_i and m_i were then calculated for each day by summing the captures of 9 traps placed in this study area. We conducted experiments monthly from May to September. In May, the flight activity of moths does not seem to mix the marked individuals evenly enough with wild individuals (see WAKAMURA et al., 1990). We therefore calculated the population estimates from June to September only. As we released insects for 3 or 4 successive days in each month, we obtained 3 or 4 estimates for each month. To obtain the average estimates, we calculated the unweighted arithmetic mean of $\hat{U}$, the unweighted geometric mean of $\hat{\phi}$ and their approximate variances:

$$\hat{\bar{U}} = \sum_{i=1}^k \hat{U}[i] / k, \quad (9)$$

$$\hat{\bar{\phi}} = \prod_{i=1}^k \hat{\phi}[i]^{(1/k)}, \quad (10)$$

$$\hat{V}(\hat{U}) = \frac{1}{k^2} \sum_{i=1}^k \hat{V}(\hat{U}[i]), \quad (11)$$

$$\hat{V}(\hat{\phi}) = \frac{\hat{\phi}^2}{k^2} \sum_{i=1}^k \frac{\hat{V}(\hat{\phi}[i])}{\hat{\phi}[i]^2}, \quad (12)$$

where k is the number of release occasions, $\hat{U}[i]$ is the i th estimate of U , and $\hat{\phi}[i]$ is the i th estimate of ϕ for each month.

The results of estimation are shown in Table 1. Estimated mean number of wild population $\hat{U}$ increased from June to September. The average rate of surviving and staying in the population $\hat{\phi}$ had the highest value in June and the lowest in August. High temperature is possibly one of the reasons why $\hat{\phi}$ diminishes in August (WAKAMURA et al., 1990).

COMPARISON WITH OTHER METHODS

To consider the validity of our method, we compared our estimates with those obtained by other methods.

The Petersen method

First, we calculated the PETERSEN estimate using the simple maximum likelihood estimate based on the binomial distribution:

$$\hat{U} = M_0 u_1 / m_1. \quad (13)$$

The variance is approximately estimated by:

$$\hat{V}(\hat{U}) = \frac{\hat{U}(\hat{U} - u_1)(u_1 + m_1)}{u_1 m_1}. \quad (14)$$

Table 1. Results of population estimation obtained by equations (4)–(8).
The average estimates were calculated using equations (9)–(12).

Release date	M_0	m_1	u_1	m_2	u_2	$\hat{U}$	$\hat{\phi}$	$\sqrt{\hat{V}(\hat{U})}$	$\sqrt{\hat{V}(\hat{\phi})}$
Jun. 16	1934	383	26	181	24	93.22	0.710	30.08	0.129
17	1968	428	24	137	20	66.39	0.602	19.92	0.099
18	2259	500	20	201	17	62.73	0.694	21.75	0.134
19	1098	215	17	73	11	62.56	0.721	26.59	0.189
average						71.22	0.680	12.45	0.069
Jul. 15	764	181	80	26	65	139.70	0.414	18.39	0.031
16	2226	466	65	121	59	153.82	0.495	26.08	0.044
17	1770	420	59	76	60	103.24	0.415	13.69	0.024
average						132.25	0.440	11.57	0.019
Aug. 21	1185	96	462	24	648	1478.47	0.259	252.34	0.030
22	1905	195	648	31	673	1617.00	0.255	189.54	0.022
23	1772	184	673	15	697	1183.17	0.183	106.45	0.013
24	1016	83	697	5	209	2411.06	0.283	816.75	0.088
average						1672.43	0.242	220.51	0.021
Sep. 11	2145	419	1356	32	1192	1959.10	0.282	82.53	0.010
12	1861	199	1192	55	1874	3151.68	0.283	300.21	0.016
13	1257	149	1874	39	1018	9491.61	0.600	1659.34	0.080
average						4867.47	0.363	562.77	0.018

Table 2. PETERSEN estimates obtained by equations (13) and (14). The average estimates were calculated using equations (9) and (11).

Release date	$\hat{U}$	$\sqrt{\hat{V}(\hat{U})}$
Jun. 16	131.29	23.83
17	110.36	20.48
18	90.36	18.18
19	86.82	19.62
average	104.71	10.32
Jul. 15	337.68	39.60
16	310.49	36.55
17	248.64	30.19
average	298.94	20.59
Aug. 21	5702.81	613.20
22	6330.46	489.89
23	6481.28	510.42
24	8531.95	949.37
average	6761.63	333.34
Sep. 11	6941.81	348.05
12	11147.30	806.70
13	15809.52	1263.40
average	11299.50	512.95

Average values and their variances were calculated for each month using equations (9) and (11), and results are shown in Table 2. The estimate of U is much larger than that obtained by equations (4) and (5). The estimate of $V(\hat{U})$ is also much larger than that obtained by equation (7). We have previously examined the problems which arise in our application of the PETERSEN method (WAKAMURA et al., 1992), and our estimates are different from those of Table 2. This is due to the difference of calculation area.

The Jolly-Seber method

Captured individuals are all removed in our experiment, which is known as a 'single-recapture census' by SEBER (1962). In this case, the JOLLY-SEBER estimations are algebraically identical with those of SEBER (1962), and we can calculate most of the estimates by the formulae of JOLLY (1965). However, we should be careful in the calculation of variances. To obtain variances, JOLLY (1965) treated immigrating populations (B_i , in JOLLY's notation) as fixed and all the N_i , n_i , s_i etc. as random variables arising from the division of each B_i . When there is artificial adding, however, some individuals in N_i , n_i , s_i etc. are those added individuals which are not B_i members. In particular, all members of released populations (s_i , in JOLLY's notation) are artificially added individuals in our experiment. We therefore treated both B_i and s_i as fixed, and calculated $\hat{V}(\hat{N}_i)$ after the modification of JOLLY (1965)'s original variance formula.

In the experiment of artificial adding, we are more interested in the wild population size U_i than the total population size N_i . The estimations of U_i and $V(\hat{U}_i)$ are more important than those of N_i and $V(\hat{N}_i)$. Although the estimates of U_i and $V(\hat{U}_i)$ are not given explicitly in JOLLY (1965), we can calculate them by the following formulae:

$$\hat{U}_i = \hat{M}_i u_i / m_i = \left(\frac{s_i Z_i}{R_i} + m_i \right) u_i / m_i, \quad (15)$$

$$\hat{V}(\hat{U}_i|U_i) = \hat{U}_i(\hat{U}_i - u_i) \left\{ \frac{\hat{M}_i - m_i + s_i}{\hat{M}_i} \left(\frac{1}{R_i} - \frac{1}{s_i} \right) + \frac{(u_i + m_i)}{u_i m_i} \right\}, \quad (16)$$

$$\hat{V}(U_i) = \hat{U}_i - \sum_{j=-1}^{i-1} \frac{\hat{U}_i(j)^2}{\hat{B}_j}, \quad (17)$$

$$\hat{V}(\hat{U}_i) = \hat{V}(\hat{U}_i|U_i) + \hat{V}(U_i), \quad (18)$$

where

- U_i : wild population size at time i ,
- s_i : number of marked individuals released at time i ,
- R_i : number of marked individuals released at time i and subsequently captured,
- B_i : number of new animals joining the population in the interval between the i and $(i+1)$ th recapture and remaining at time $i+1$, and $B_{-1} = U_0 = N_0$,
- $U_i(j)$: expected number in U_i which first joined the population as members of B_j ,
- Z_i : number of animals marked before time i which are not captured at time i but are captured subsequently.

Our notation for animals first released at time 0 is different from JOLLY's notation.

$\hat{V}(\hat{U}_i|U_i)$ is the estimated variance due to error of estimation in $\hat{U}_i$, and $\hat{V}(U_i)$ is the estimated variance of the conditional parameter U_i due to the probabilistic process. The variance of estimate $\hat{U}_i$, i.e., $V(\hat{U}_i)$, can be estimated by the sum of these two variances. The last term of $\hat{V}(\hat{U}_i|U_i)$ is the same as equation (14) of the PETERSEN estimate, which represents the sampling variance due to m_i . The remaining term of $\hat{V}(\hat{U}_i|U_i)$ represents the error due to the estimation of M_i . The probabilistic variance, $\hat{V}(U_i)$, is usually much smaller than the conditional variance $\hat{V}(\hat{U}_i|U_i)$. However, $\hat{V}(U_i)$

Table 3. JOLLY-SEBER estimates obtained by equations of JOLLY (1965) and equation (15). The average estimates of U_i and ϕ_i were calculated using equations (9) and (10), respectively.

Date	$\hat{U}_i$	$\hat{N}_i$	$\hat{B}_i$	$\hat{\phi}_i$
Jun. 16	—	—	—	0.600
17	78.72	1238.40	29.35	0.529
18	57.26	1510.35	34.26	0.593
19	54.00	1895.38	—	—
average	63.33			0.573
Jul. 15	—	—	—	0.403
16	136.08	443.97	111.47	0.438
17	136.01	1165.52	—	—
average	136.05			0.420
Aug. 21	—	—	—	0.317
22	1810.21	2186.35	1611.38	0.315
23	2035.90	2723.96	1526.86	0.282
24	1918.86	2551.82	—	—
average	1921.66			0.305
Sep. 11	—	—	—	0.362
12	2512.54	3288.90	3859.07	0.375
13	4292.79	5124.69	—	—
average	3402.66			0.386

Table 4. Estimated variances of JOLLY-SEBER estimates obtained by equations of JOLLY (1965) and equations (16)–(18). The variances of average estimates of U_i and ϕ_i were estimated using equations (11) and (19), respectively.

Date	$\sqrt{\hat{V}(\hat{U}_i)}$	$\sqrt{\hat{V}(\hat{N}_i)}$	$\sqrt{\hat{V}(\hat{B}_i)}$	$\sqrt{\hat{V}(\hat{\phi}_i)}$	$\sqrt{\hat{V}(\hat{U}_i U_i)}$	$\sqrt{\hat{V}(\hat{N}_i N_i)}$
Jun. 16	—	—	—	0.0270	—	—
17	14.14	56.93	12.09	0.0221	13.45	52.51
18	10.32	58.89	11.59	0.0276	9.28	51.32
19	10.71	84.65	—	—	9.97	78.62
average	6.84	—	—	0.0112	—	—
Jul. 15	—	—	—	0.0303	—	—
16	15.46	32.96	15.50	0.0206	14.37	29.49
17	14.80	54.46	—	—	14.07	48.42
average	10.70	—	—	0.0174	—	—
Aug. 21	—	—	—	0.0423	—	—
22	288.49	327.71	222.97	0.0332	287.81	326.72
23	239.85	299.27	230.49	0.0369	239.13	297.87
24	264.39	335.93	—	—	263.76	334.72
average	152.99	—	—	0.0188	—	—
Sep. 11	—	—	—	0.0253	—	—
12	187.83	232.50	413.64	0.0332	186.28	230.18
13	436.50	492.63	—	—	436.07	491.68
average	237.60	—	—	0.0183	—	—

becomes important when the sampling fraction (n_i/N_i) approaches one, because $\hat{V}(\hat{U}_i|U_i)$ becomes very small in such a case. To calculate $\hat{V}(N_i)$ or $\hat{V}(U_i)$, we need the value of $N_0 (=U_0)$, which cannot be estimated. JOLLY (1965) therefore assumed that $N_0 (=U_0)=N_1$ in his calculation. When there is artificial adding, however, such an assumption will not be applicable. Here, we adopted the assumption that $N_0 (=U_0)=U_1$. We calculated the average estimates for each month using the equations (9)–(11) and the following equation:

$$\hat{V}(\hat{\phi}) = \frac{\hat{\phi}^2}{k^2} \left\{ \sum_{i=1}^k \frac{\hat{V}(\hat{\phi}[i])}{\hat{\phi}[i]^2} + 2 \sum_{i=1}^{k-1} \frac{\text{cov}(\hat{\phi}[i], \hat{\phi}[i+1])}{\hat{\phi}[i] \hat{\phi}[i+1]} \right\}. \quad (19)$$

The results are listed in Tables 3 and 4. The population estimates show rather good agreement with those obtained by equations (4) and (5).

DISCUSSION

We proposed a basic method which can be applied to a 'single-release single-recapture' experiment in which sampling censuses are conducted only twice. We considered the validity of our estimates by comparing them with those obtained by the PETERSEN and JOLLY-SEBER methods. Among these three methods, the JOLLY-SEBER's is based on the least restricted assumptions, and seems to give the most accurate estimates in many cases. In our experiments, as indicated in Tables 2 and 3, the PETERSEN estimates are much larger than the JOLLY-SEBER estimates, suggesting large biases in the former. On the other hand, the estimates obtained by our method showed

satisfactory agreement with those obtained by the JOLLY-SEBER method (Tables 1 and 3) (although our method requires only one more sampling census to be added to the PETERSEN method while the JOLLY-SEBER method requires one more sampling census and one more release procedure to be added). In conclusion, our method seems to be useful from a practical point of view.

However, the assumptions of the model should be carefully discussed. Generally, there is a possibility that the ϕ from the release to the first sampling and the ϕ from the first sampling to the second sampling are different, because the released animals may show different behavior just after release. In our experiments in particular, the first sampling began just after the release of marked insects, and the ϕ -value in the interval from the release to the first sampling seems to be mainly determined by the proportion of individuals which do not emigrate in the first evening. On the other hand, the ϕ -value in the interval from the first sampling to the second sampling seems to be determined by two factors; the survival rate from the first evening to the second evening and the proportion of individuals which do not emigrate in the second evening. Therefore, assumption (2) mentioned above, that ϕ is constant irrespective of duration, may be somewhat doubtful in our experiments if, for example, daytime mortality is significant.

To examine the bias due to the lack of validity in assumptions, we should consider a model based on less restrictive assumptions. We let ϕ_0 be the ϕ value from the release to the first sampling census, and ϕ_1 be that from the first to the second sampling census. Then, we obtain the following relations:

$$\begin{aligned} M_1 &= \phi_0 M_0, \\ M_2 &= \phi_1 (\phi_0 M_0 - m_1), \\ U_2 &= \phi_1 (U_1 - u_1) + B_1. \end{aligned}$$

If we estimate M_1 by the product of equation (4) and M_0 , the approximate expectation is:

$$E(\hat{M}_1) \approx \frac{\phi_1}{\phi_0} \frac{U_1}{\phi_1 (U_1 - u_1) + B_1} (M_1 - m_1) + m_1.$$

Assumption (1) in the estimation states that $\phi_1 (U_1 - u_1) + B_1 = U_1$, and assumption (2) states that $\phi_1 = \phi_0$. Bias in $\hat{U}$ depends on the bias in $\hat{M}_1$. So, we can see that we are liable to underestimate U_1 if $\phi_1 < \phi_0$, and overestimate it if $\phi_1 > \phi_0$. We are also liable to overestimate U_1 if $\phi_1 (U_1 - u_1) + B_1 < U_1$, i.e., if immigration is insufficient to compensate for the artificial removal by traps, or if immigration is insufficient to compensate for population reduction by natural emigration or death. In our experiment, ϕ_0 seems to be larger than ϕ_1 as discussed above, so we must consider the possibility of underestimation. In our experiments in June, the rate of trapping seems to be high enough to reduce the wild population size (see WAKAMURA et al., 1990). So the possibility of overestimation should be noted in June. On the other hand, the estimated wild population size shows the trend of increase in August, so we should consider the possibility of underestimation in August.

We evaluated the validity of our present method by comparing the estimates with those obtained by the JOLLY-SEBER method. However, the estimates obtained by the JOLLY-SEBER method are also subject to bias. The approximate expectation of their

estimate of M_1 is:

$$E(\hat{M}_1) \approx \frac{\phi_1}{\phi_0} (M_1 - m_1) + m_1.$$

Therefore, if $\phi_1 < \phi_0$, the JOLLY-SEBER method also underestimates U_1 . MANLY and PARR (1968) considered a method which is applicable even if the survival rates are different among released populations depending on their age-class. However, their method is applicable only if the recaptured insects can be released again. When we use traps which kill all of the recaptured insects, their method is not applicable and we should consider the application of another method. In our previous paper, we reported the results of population estimation obtained by the method of HARTSTACK et al. (1971) (WAKAMURA et al., 1992). The estimated wild population densities (per ha) for June, July, August, September were 0.009, 0.031, 0.60 and 2.00, respectively. The population estimates in the 6 km diameter circle are 25.5, 87.7, 1696.5 and 5654.9, respectively. Table 1 shows that the population estimates for August and September obtained by our present method are similar to those obtained by the method of HARTSTACK et al. (1971), although their calculations are based on much different assumptions.

ACKNOWLEDGEMENTS

We are grateful to Prof. E. KUNO of Kyoto University for helping with the derivation of the equation, and to Prof. F. NAKASUJI of Okayama University for encouraging the work.

REFERENCES

- HAMADA, R. (1976) Density estimation by the modified JACKSON's method. *Appl. Entomol. Zool.* **11**: 194-201.
- HARTSTACK, A. W. JR., J. P. HOLLINGSWORTH, R. L. RIDGWAY and H. H. HUNT (1971) Determination of trap spacings required to control an insect population. *J. Econ. Entomol.* **64**: 1090-1100.
- JOLLY, G. M. (1965) Explicit estimates from capture-recapture data with both death and immigration—Stochastic model. *Biometrika* **52**: 225-247.
- MANLY, B. F. J. and M. J. PARR (1968) A new method of estimating population size, survivorship, and birth rate from capture-recapture data. *Trans. Soc. Brit. Entomol.* **18**: 81-89.
- PARKER, R. A. (1963) On the estimation of population size, mortality, and recruitment. *Biometrics* **19**: 318-323.
- SEBER, G. A. F. (1962) The multi-sample single recapture census. *Biometrika* **49**: 339-350.
- SEBER, G. A. F. (1982) *The Estimation of Animal Abundance and Related Parameters*. 2nd ed. Griffin, London. 654 pp.
- WAKAMURA, S., S. KOZAI, K. KEGASAWA and H. INOUE (1990) Population dynamics of adult *Spodoptera litua* (FABRICIUS) (Lepidoptera: Noctuidae): Dispersal distance of male moths and its seasonal change. *Appl. Entomol. Zool.* **25**: 447-456.
- WAKAMURA, S., S. KOZAI, K. KEGASAWA and H. INOUE (1992) Population dynamics of adult *Spodoptera litura* (FABRICIUS) (Lepidoptera: Noctuidae): Estimation of male density by using release recapture data. *Appl. Entomol. Zool.* **27**: 1-10.