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Estimating the Population Size for Capture–Recapture Data with Unequal Catchability

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SUMMARY

A point estimator and its associated confidence interval for the size of a closed population are proposed under models that incorporate heterogeneity of capture probability. Real data sets provided in Edwards and Eberhardt (1967, *Journal of Wildlife Management* **31,** 87–96) and Carothers (1973, *Journal of Animal Ecology* **42,** 125–146) are used to illustrate this method and to compare it with other estimates. The performance of the proposed procedure is also investigated by means of Monte Carlo experiments. The method is especially useful when most of the captured individuals are caught once or twice in the sample, for which case the jackknife estimator usually does not work well. Numerical results also show that the proposed confidence interval performs satisfactorily in maintaining the nominal levels.

1. Introduction

The capture–recapture method has been widely used by field biologists and ecologists to investigate the dynamics of biological populations. For a closed population, the classical problem for capture–recapture experiments is the estimation of the population size. The reader is referred to Cormack (1968, 1979), Otis et al. (1978), Pollock (1981), and Seber (1982, 1986) for a general comprehensive review on this topic.

Most of the previous works are based on the assumption that all the individuals of the population have the same capture probabilities. However, as indicated in the ecological literature (e.g., Young, Neess, and Emlen, 1952; Tanaka, 1956; Crowcroft and Jeffers, 1961; Tanton, 1965; Eberhardt, 1969; Carothers, 1973; Wilbur and Landwehr, 1974), individual heterogeneity of capture probability may arise in many ways in biological populations. Eberhardt (1969, p. 28) pointed out that various sets of data showed the equal-probability-of-capture assumption is often not valid. Carothers (1973, p. 146) found that it was impossible to achieve equal catchability even with randomized capture locations on each sampling occasion. He further concluded that equal catchability is an unattainable ideal in natural populations. Many previous studies (e.g., Edwards and Eberhardt, 1967; Carothers, 1973; Otis et al., 1978; Burnham and Overton, 1979) have confirmed that the usual "Schnabel"-type estimators (Schnabel, 1938; Schumacher and Eschmeyer, 1943) based on the equal-catchability assumption are negatively biased by heterogeneity of capture probabilities.

Some estimators without the equal-catchability restriction have been proposed by Eberhardt, Peterle, and Schofield (1963), Tanaka (1967), Eberhardt (1969), and Marten (1970). Tanaka and Marten used regression-type estimators by assuming a certain form of unequal capture probabilities, while Eberhardt et al. fitted the capture frequency counts as a

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geometric series. These two types of estimation procedures along with the usual Schnabel-type estimators were applied by Carothers (1973) to some real data sets where the true population size is known. (We will also discuss these data sets in Section 3.) He reported that these two types of estimators failed to reduce significantly the magnitude of the bias of the usual Schnabel-type estimators. Pollock (in a 1974 Ph.D. thesis at Cornell University, and 1976, 1981) pioneered the work by considering models where heterogeneity of capture probability is allowed. Burnham and Overton (1978, 1979) rigorously introduced a heterogeneity model by assuming that individual capture probability is a random variable from an arbitrary distribution. They also derived the jackknife estimator, which has been extensively investigated in Otis et al. (1978) and White et al. (Los Alamos National Laboratory Report LA-8787-NERP, 1982) using many real and simulated data sets. They found that the jackknife estimator is the most robust one among others considered therein. Pollock and Otto (1983) presented a range of new estimators for the heterogeneity model and the heterogeneity and trap-response model. Based on numerical comparisons, they support the use of the jackknife estimator for the heterogeneity model. The jackknife estimator generally produces adequate estimates if many individuals are caught a relatively large number of times (Otis et al., 1978, p. 35).

On the other hand, the jackknife estimator usually underestimates the population size if many individuals have very small capture probabilities so that they are caught only once or twice in the multiple-recapture experiments. [This is clearly seen from Table 1a of Pollock and Otto (1983) for the cases that the number of trapping days is less than 15.] The last concern is precisely what motivated the present study. In Section 2, we will propose an estimator and its associated confidence interval for the population size under the heterogeneity model. This estimator will be shown to be useful when many captured individuals are caught only a few times in the sample. Some real data sets are used to compare the present estimator with other previous results in Section 3. In the same section, results from a limited Monte Carlo simulation further show the performance of the proposed method.

2. Model and Estimator

We first describe the heterogeneity model developed in Burnham and Overton (1978, 1979). Assume the population is closed with size N and there are t trapping occasions. Let the individuals be indexed by $1, \ldots, N$ and p_{ij} be the capture probability of the ith individual on the jth trapping occasion, $i = 1, \ldots, N$ and $j = 1, \ldots, t$. We further assume $p_{ij} = p_i$ for $j = 1, \ldots, t$, and $p_1, \ldots, p_N$ are a random sample from a probability distribution F. The data consist of an $N \times t$ matrix $\mathbf{X} = (X_{ij})$, where

$$X_{ij} = I[\text{the } i\text{th individual is caught in } j\text{th trapping occasion}]$$

and $I[A]$ is the usual indicator function—that is, $I[A] = 1$ if event A occurs, 0 otherwise. We assume X_{ij}, $i = 1, \ldots, N$ and $j = 1, \ldots, t$, are mutually independent. Let

$$S = \sum_{i=1}^{N} I\left[\sum_{j=1}^{t} X_{ij} \geqslant 1\right]$$

denote the number of distinct individuals caught in the experiment, and

$$f_k = \sum_{i=1}^{N} I\left[\sum_{j=1}^{t} X_{ij} = k\right], \quad k = 0, 1, \ldots, t,$$

be the number of individuals captured exactly k times in the t samples. It is clear that only S rows in the data matrix are observed and f_0 represents the number of unobserved individuals, with $N = S + f_0$. It follows from Burnham and Overton (1978) that $(f_1, \ldots, f_t)$ are sufficient statistics under this model and the joint, unconditional distribution function of $(f_0, f_1, \ldots, f_t)$ is a multinomial, that is,

$$p(f_0, f_1, \ldots, f_t) = \binom{N}{f_0\, f_1 \ldots f_t} \prod_{i=0}^{t} [\theta_i(F)]^{f_i}, \tag{1}$$

where

$$\theta_i(F) = \int_0^1 \binom{t}{i} p^i(1-p)^{t-i}\, dF(p).$$

Using the generalized jackknife technique, Burnham and Overton (1978) derived the kth-order jackknife estimator, $\tilde{N}_{\mathrm{J}k}$, which is a linear function of f_i:

$$\tilde{N}_{\mathrm{J}k} = \sum_{i=1}^{t} a_{ik} f_i.$$

For coefficients a_{ik}, the reader is referred to Burnham and Overton (1978, 1979) for details. They also provided a testing procedure to select an appropriate k. Usually k is chosen to be less than 5.

Under the same model, we now proceed to obtain an alternative estimator of N. From (1), we have

$$\mathrm{E}(f_i) = N \int_0^1 \binom{t}{i} p^i(1-p)^{t-i}\, dF(p), \quad i = 0, 1, \ldots, t. \tag{2}$$

If t is large and p is small, it follows that

$$\mathrm{E}(f_i) \approx N \int_0^1 [(tp)^i e^{-tp}/i!]\, dF(p), \quad i = 0, 1, \ldots, t. \tag{3}$$

Note here that for any $p \geqslant p^*$ for some p^* such that the Poisson approximation is not good, (3) is still valid as long as $\int_{p^*}^1 dF(p)$ is small.

Consider the following cumulative distribution function in $[0, t]$:

$$G(u) = \int_0^u x e^{-x}\, dF\!\left(\frac{x}{t}\right) \Big/ \int_0^t x e^{-x}\, dF\!\left(\frac{x}{t}\right). \tag{4}$$

Then from (3) and (4),

$$\begin{aligned} \mathrm{E}(f_0) &\approx N \int_0^1 e^{-tp}\, dF(p) \\ &\approx [\mathrm{E}(f_1)] \int_0^t u^{-1}\, dG(u). \end{aligned} \tag{5}$$

The kth moment μ_k of G is given by

$$\begin{aligned} \mu_k &= \int_0^t u^k\, dG(u) \\ &= \int_0^1 (tx)^{k+1} e^{-tx}\, dF(x) \Big/ \int_0^1 (tx)e^{-tx}\, dF(x) \\ &\approx (k+1)!\, \mathrm{E}(f_{k+1})/\mathrm{E}(f_1). \end{aligned} \tag{6}$$

Replacing $\mathrm{E}(f_i)$ by f_i in the above expression, we obtain the following moment estimator of μ_k if $f_1 \neq 0$:

$$m_k = (k + 1)!\, f_{k+1}/f_1. \tag{7}$$

Using Jensen's inequality, we have from (5) and (6) that

$$\mathrm{E}(f_0) \geq \mathrm{E}(f_1)/\mu_1 = [\mathrm{E}(f_1)]^2/[2\mathrm{E}(f_2)].$$

Therefore, a lower bound $\hat{N}$ of the population size is readily obtained as

$$\hat{N} = S + f_1^2/(2f_2). \tag{8}$$

When the first two moment estimates m_1 and m_2 are legitimate moments of distributions in $[0, t]$—namely, m_1 and m_2 satisfy $t^2 > tm_1 > m_2 > m_1^2$—we are mainly interested in finding an estimator $\hat{G}$ of G such that $\hat{G}(x)$ has m_1, m_2 as its first two moments. Our approach is similar to that taken by Harris (1959), who dealt with other statistical problems. Let $C(m_1, m_2)$ denote the class of cumulative distribution functions in $[0, t]$ with m_1, m_2 as the first two moments. Harris (1959) proved that

$$\min_{G \in C} \int u^{-1}\, dG(u) = \int u^{-1}\, dH(u),$$

where

$$H(u) = \begin{cases} 0, & u < (tm_1 - m_2)/(t - m_1) \\ (t - m_1)^2[(t - m_1)^2 + m_2 - m_1^2]^{-1}, & (tm_1 - m_2)/(t - m_1) \leq u < t. \\ 1, & t \leq u \end{cases}$$

Hence, we obtain a lower bound $\hat{N}_{\min}$ of N:

$$\begin{aligned} \hat{N}_{\min} &= S + \int u^{-1}\, dH(u) \\ &= S + f_1[(t - m_1)^2 + m_2 - m_1^2]^{-1}[(t - m_1)^3(tm_1 - m_2)^{-1} + (m_2 - m_1^2)t^{-1}]. \end{aligned} \tag{9}$$

A simple approximation formula of (9) (courtesy of Professor Richard Cormack) is

$$\hat{N}_{\min} \approx \hat{N}_1 = S + \frac{f_1^2}{2f_2}\left[\frac{1 - m_1/t}{1 - m_2/(tm_1)}\right]. \tag{10}$$

This provides a "correction factor" for $\hat{N}$ and it is clear that $\hat{N}_1 \geq \hat{N}$ under the moment restrictions. Also, notice that when the magnitude of m_1 and m_2 are relatively small compared to that of t, the value of $\hat{N}_{\min}$ is very close to $\hat{N}$. Both $\hat{N}$ and $\hat{N}_1$ are applied to the real data sets in the next section. We found that in practice there will often be little difference in the two estimates if $\hat{N}_1$ exists. Hence, we will concentrate mainly on the performance of the estimator $\hat{N}$ in the simulation comparisons. $\hat{N}$ is actually a lower bound of N subject to the moment constraints. However, its performance as an estimator of N is encouraging and competitive with other estimators, as will be seen in the next section.

A similar technique has been applied by the author (Chao, 1984) to estimate the number of species under a quite different model. The model considered there does not allow the author to derive an analytic variance estimator. So the percentile method based on the bootstrap method (Efron, 1979, 1981, 1982) was employed in that work to construct confidence intervals. However, under the heterogeneity model, we are able to provide the following variance estimator by a standard asymptotic approach:

$$\hat{\sigma}^2 = \mathrm{var}_{\mathrm{est}}(\hat{N}) = f_2[.25(f_1/f_2)^4 + (f_1/f_2)^3 + .5(f_1/f_2)^2].$$

(An approximate variance formula for $\hat{N}_1$ can be analogously obtained.) Assuming the normality of $\hat{N}$, we have a classical approximate 95% confidence interval:

$$[\hat{N} - 1.96\hat{\sigma},\ \hat{N} + 1.96\hat{\sigma}]. \tag{11}$$

Burnham (personal communication) suggested using a log-transformation to get an improved confidence interval. That is, we treat $\log(\hat{N} - S)$ as an approximately normal random variable, which gives a 95% interval as

$$[S + (\hat{N} - S)/C,\ S + (\hat{N} - S)C], \tag{12}$$

where

$$C = \exp\{1.96[\log(1 + \hat{\sigma}^2/(\hat{N} - S)^2)]^{1/2}\}.$$

Both intervals will be applied to the data sets and simulation study discussed in the next section.

It should be emphasized that the proposed procedure relies on the condition that t is "large" and the p_i are "small." It is generally recommended, from some simulation results, that the number of samples be at least 5. When most p_i are relatively small, all individuals are likely to be captured only a few times in the capture–recapture sampling. Thus, the information should be mainly concentrated on the lower-order frequency counts, which are exactly those needed to construct moment estimators. If $(f_3, f_4, \ldots)$ carry nonnegligible information, our estimator can be regarded only as a lower bound of the population size.

3. Examples

3.1 *Cottontail Data*

Edwards and Eberhardt (1967) conducted a live-trapping study on a confined population of known size. In their study, 135 wild cottontail rabbits were penned in a 4-acre rabbit-proof enclosure. Live trapping was conducted for 18 consecutive nights. Recorded capture frequencies (f_1 to f_7) were

$$43,\quad 16,\quad 8,\quad 6,\quad 0,\quad 2,\quad 1.$$

Edwards and Eberhardt reported that the usual Schnabel-type estimates were considerably less than the true parameter 135 (e.g., the Schnabel estimate is 96; the Schumacher and Eschmeyer estimate is 97). The corresponding confidence intervals were thus not satisfactory either. They suggested modelling the capture frequency data by a geometric series and obtained estimates 136 and 164 by two different estimation procedures. Burnham and Overton (1978, 1979) suggested using the third-order jackknife estimate, 159, with a 95% confidence interval (116, 202). They further recommended an improved, interpolated estimate of 142 and the interval (112, 172). The proposed estimator in this work gives $\hat{N} =$ 134 and formula (11) yields an approximate confidence interval (87, 181). The log-transformation leads to the interval (103, 202). Although for this example the transformed interval seems less satisfactory than the classical one, in most of the other cases discussed later, it has better performance in coverage probability. Since m_1 and m_2 for this data are legitimate moments, we consequently obtain the estimate $\hat{N}_1 = 136$, with a 95% confidence interval (87, 185), which agree well with the results of $\hat{N}$.

3.2 *Taxicab Data*

Carothers (1973) provided a very valuable data set by conducting a capture–recapture experiment on the taxicab population of Edinburgh, Scotland. As with the cottontail data, this study has the advantage of known population size (420), yet the population is an actual

Table 1
Comparison of estimates for Carothers (1973) data, true value $N = 420$, $t = 5$

Sampling scheme	Data subset	f_1	f_2	f_3	f_4	Jackknife method Estimate	Jackknife method Interval	Proposed method $\hat{N}$	Proposed method $\hat{N}_1$	Proposed method Interval (11)	Proposed method Interval (12)
A	a	65	12	0	0	192	(155, 299)	253	*	(119, 387)	(162, 444)
	b	73	8	0	0	217	(176, 258)	414	*	(135, 693)	(230, 825)
	c	75	7	0	0	223	(182, 264)	484	*	(133, 835)	(256, 1007)
	d	109	24	3	0	325	(274, 376)	384	*	(244, 523)	(279, 566)
	e	112	28	2	0	332	(281, 383)	366	*	(245, 487)	(274, 523)
	f	117	24	4	0	350	(297, 403)	430	436	(273, 588)	(311, 635)
	g	135	42	9	1	407	(350, 464)	404	405	(302, 506)	(323, 533)
B	a	78	5	0	0	233	(190, 276)	691	*	(92, 1291)	(323, 1626)
	b	67	9	0	0	199	(160, 238)	325	*	(121, 530)	(190, 624)
	c	71	7	1	0	213	(172, 254)	439	457	(122, 756)	(234, 914)
	d	112	22	0	2	333	(282, 384)	421	*	(258, 584)	(299, 635)
	e	106	28	3	0	315	(266, 364)	338	*	(228, 448)	(254, 481)
	f	102	26	3	0	303	(250, 356)	331	*	(218, 444)	(246, 479)
	g	116	48	6	2	346	(307, 385)	312	*	(244, 381)	(259, 399)

* The first two moments are not legitimate.

one as opposed to simulated data. The reader may refer to Carothers (1973) for details of the population and of different methods of sampling. Applying various capture–recapture models, Carothers obtained several estimates under both equal- and unequal-catchability assumptions. As expected, the majority of the estimates based on equal catchability were much below the known population size. Also, no method based on unequal catchability was found to lead to a noticeable decrease in the bias. A portion of the collected data is tabulated in Table 1, where the sampling schemes and data subsets are the ones Carothers identifies in his paper. These data sets are typical in that most captured individuals were caught only a few times. The resulting noninterpolated jackknife, the present estimate $\hat{N}$, $\hat{N}_1$ (if it exists), and the associated confidence intervals based on $\hat{N}$ are given in the same table for comparison. For these data subsets, our estimator is generally preferable to the jackknife or other estimators considered in Carothers (1973), because it is on average closer to the true parameter of 420. The use of a log-transformation in all cases shifts the original interval rightward and results in some increases in interval length, which usually leads to improvements in coverage probabilities, as will be seen in the simulation study. In general, our confidence intervals are much wider than the jackknife intervals (since the standard errors are always larger), but more of the intervals include the true value. Out of the 14 cases, there are only three data subsets (f and g for sampling scheme A and subset c for sampling scheme B) for which the first two moments satisfy the restrictions for calculating $\hat{N}_1$. The resulting estimates of $\hat{N}_1$ are generally close to those of $\hat{N}$.

3.3 *Simulation Study*

As indicated in Otis et al. (1978), a common difficulty for various estimators of population size is the poor confidence interval coverage. To understand whether the proposed confidence intervals have the same difficulty, we carried out a limited simulation study. Several populations representing varying degrees of heterogeneity were considered in this work; they are described in Table 2. We specifically chose populations with small average capture probability being .05 or .1. For each given population we produced 100 simulation runs with $t = 5$, 7, and 10. Then for each generated data set, the point estimate, its standard error, and the corresponding confidence interval were computed for (noninterpolated) jackknife and the proposed $\hat{N}$ in (8). In the calculation of the jackknife estimates, we follow the testing procedure in Burnham and Overton (1978, 1979) to select an appropriate order

Table 2
Description of populations used in simulation

Population	N	$p_i, i = 1, \ldots, N$	$E(p)$
1	400	$p_i = .02, i = 1, \ldots, 200; p_i = .08, i = 201, \ldots, 400$	.05
2	400	$p_i = .02, i = 1, \ldots, 100; p_i = .04, i = 101, \ldots, 300;$ $p_i = .1, i = 301, \ldots, 400$	.05
3	400	$p_i = .02, i = 1, \ldots, 100; p_i = .03, i = 101, \ldots, 200;$ $p_i = .07, i = 201, \ldots, 300; p_i = .08, i = 301, \ldots, 400$	.05
4	400	$p_i = .01, i = 1, \ldots, 80; p_i = .03, i = 81, \ldots, 160;$ $p_i = .05, i = 161, \ldots, 240; p_i = .07, i = 241, \ldots, 320;$ $p_i = .09, i = 321, \ldots, 400$	.05
5	200	$p_i \sim$ Uniform(0, .1)	.05
6	200	$p_i \sim .2 \times$ Beta(1, 3)	.05
7	200	$p_i \sim$ Uniform(0, .2)	.1
8	200	$p_i \sim .2 \times$ Beta(2, 2)	.1

of the jackknife estimator up to the fifth order. Finally, these 100 estimates and standard errors were averaged and the coverage probabilities were estimated.

The simulation results are given in Table 3. Generally, there is a tendency for the standard error of the jackknife estimator to increase as t increases, while the standard error of the

Table 3
Simulation results for populations of Table 2 (100 *trials*)

			Jackknife method			Proposed method			
Population	N	t	Estimate	s.e.	Coverage (%)	Estimate	s.e.	Coverage (%)	Coverage (%, transf.)
1	400	5	229	21.5	0	405	131.8	88	95
		7	310	30.4	17	357	79.8	84	91
		10	340	46.4	70	355	56.7	79	88
2	400	5	228	21.5	0	410	139.6	87	94
		7	315	31.0	25	367	82.1	83	91
		10	342	44.7	66	349	54.3	71	81
3	400	5	228	21.9	0	438	148.7	90	95
		7	328	31.2	39	399	93.2	87	92
		10	368	44.0	82	362	56.1	79	88
4	400	5	229	21.5	0	398	127.3	91	96
		7	318	30.9	29	371	82.6	92	92
		10	347	44.0	71	345	52.8	72	83
5	200	5	112	15.1	0	212	115.0	95	99
		7	162	22.9	64	188	71.2	93	97
		10	189	25.2	73	176	49.9	88	99
6	200	5	95	13.8	0	193	115.6	75	86
		7	133	19.0	12	158	55.0	63	79
		10	152	22.3	50	152	37.1	57	74
7	200	5	168	18.4	57	184	42.1	77	89
		7	173	25.0	75	176	26.7	71	78
		10	189	19.7	87	173	19.2	48	73
8	200	5	179	19.0	77	210	51.5	91	95
		7	184	27.4	89	192	32.3	90	95
		10	208	21.3	86	190	22.2	83	89

proposed estimator decreases with t. The empirical coverage probabilities of the interval (12) using a log-transformation are always closer to the anticipated level .95 than the classical interval (11). Hence, it is recommended for practical use. For $t = 5$ and 7, the jackknife estimator has considerably smaller standard errors, but the estimates in several cases are severely negatively biased. Also, the coverage probabilities are much lower than the nominal level, especially when the average capture probability is .05. The proposed method produces reasonable estimates with higher coverage probabilities, although the precision is quite low. As t is increased to 10, there is substantial improvement in the jackknife results, which usually perform better than the proposed estimates. Actually, when t becomes large, some individuals would be captured increasingly more times; hence, more information is spread out to the other capture frequencies, i.e., $(f_3, f_4, \ldots)$. As expected, our estimates appear to have some negative bias. We finally remark that if the average capture probability is relatively large [for example, capture probability is a random variable from uniform (0, 1) or beta (2, 2) etc.], the present method will fail to work. Research on extensions is ongoing.

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Résumé

Un estimateur ponctuel, et son intervalle de confiance associé, de la taille d'une population fermée sont proposés sous différents modèles tenant compte de l'hétérogénéité des probabilités de capture. Des jeux de données réelles provenant de Edwards et Eberhardt (1967, *Journal of Wildlife Management* **31,** 87–96) et de Carothers (1973, *Journal of Animal Ecology,* **42,** 125–146) sont utilisés pour illustrer cette méthode et pour la comparer à d'autres. On examine aussi les performances de la procédure proposée par la méthode de Monte-Carlo. Cette méthode est particulièrement utile quand la majorité des individus capturés le sont une ou deux fois, situation telle que l'estimateur jackknife ne marche généralement pas bien. Des résultats numériques montrent que l'intervalle de confiance proposé donne satisfaction en respectant les niveaux annoncés.

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