ESTIMATING ANIMAL ABUNDANCE WITH CAPTURE FREQUENCY DATA

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Abstract: I describe a new method for estimating the number of animals in a closed population with capture–recapture data under a heterogeneity model. The model is applied to capture frequency records of striped skunk (*Mephitis mephitis*), eastern chipmunk (*Tamias striatus*), eastern cottontail (*Sylvilagus floridanus*), and taxicab populations. I also report the results of a Monte Carlo simulation to assess the relative merits of the proposed moment estimator and the jackknife estimator. If many individuals are caught more than twice, the jackknife estimator is superior to the proposed moment estimator. However, when the mean capture probability is small, so that most captured animals are caught only 1–2 times in the samples, the moment estimator is usually less biased than the jackknife estimator. The mean coverage probability of the confidence interval associated with the moment estimator is also closer to the nominal level than that of the jackknife interval.

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My study considers the problem of comparing estimators of population size in a multiple capture–recapture experiment under the model that incorporates heterogeneity of capture probabilities; i.e., individuals have different but constant probabilities of capture over trapping samples (Burnham and Overton 1978, 1979). The population is assumed to be closed so that there are no changes due to birth, death, emigration, or immigration during the sampling period. Refer to Cormack (1968, 1979), Otis et al. (1978), and Seber (1982, 1986) for a general review of various models and estimators currently in use.

Most of the previous methods for deriving population estimates generally require that all animals have the same capture probabilities. Edwards and Eberhardt (1967), Carothers (1973), Otis et al. (1978), and Burnham and Overton (1979) have examined the biases arising from a failure of this assumption and confirmed that heterogeneity can cause substantial bias in the estimators when assuming equal catchability. For example, Edwards and Eberhardt (1967) conducted a livetrapping experiment on a confined eastern cottontail population of known size. They found that the usual Schnabel estimates (Schnabel 1938, Schumacher and Eschmeyer 1943) were considerably lower than the true population size. A similar finding was reported by Carothers (1973), who conducted a unique study on the taxicab population, in Edinburgh, United Kingdom. Mares et al. (1981) estimated the abundance of eastern chipmunks using a capture–recapture technique and found that 3 commonly used estimators always underestimated the known abundance. Greenwood et al. (1985) recently provided a data set from striped skunk populations of known sizes. They made numerical comparisons of 10 different estimators under several models and found all underestimated true population size. These data sets will be considered in the following sections.

Burnham and Overton (1978, 1979) introduced a heterogeneity model by assuming that the individual capture probability is a random sample from an arbitrary distribution function. They also derived the jackknife estimators (of several orders), which have been extensively studied by Otis et al. (1978) using many real and simulated data sets. Pollock and Otto (1983) subsequently supported the use of the jackknife estimator based on some numerical comparisons. Greenwood et al. (1985) also concluded that the jackknife estimator produced the best estimates of skunk abundance. In general, the jackknife estimator works well if most individuals are captured many times. However, if many animals have very small capture probabilities, the jackknife estimator will have a negative bias, as will every other known estimator (White et al. 1982:65).

Chao (1984, 1987) derived an alternative approach more appropriate for data sets with only low-order capture frequencies. In the following sections, the new moment estimator will be reviewed and applied to real data sets (Edwards and Eberhardt 1967, Carothers 1973, Mares et al. 1981, Greenwood et al. 1985). A Monte Carlo simulation study that suggests guidelines for choosing an estimator is also provided.

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Table 1. Comparison of 4 population size estimators for striped skunks (Greenwood et al. 1985).

Capture frequencies	1977 (8 trap-nights) F	1977 M	1977 Both	1978 (4 trap-nights) F	1978 M	1978 Both
f_0	1	3	4	7	4	11
f_1	2		2	7	3	10
f_2	4	3	7	3	1	4
f_3	2	3	5	1		1
f_4	1	2	3	2		2
f_5		2	2			
S[a]	9	10	19	13	4	17
Known N	10	13	23	20	8	28
Schnabel[b]	11.00 ± 3.65[c]	10.91 ± 2.39	21.38 ± 3.79	14.82 ± 4.92	6.00 ± 29.13	20.33 ± 6.40
Jackknife[d]	10.75 ± 1.81	10.00 ± 0.00	20.75 ± 1.81	18.25 ± 3.03	6.25 ± 1.98	24.50 ± 3.62
Moment $\hat{N}$	9.50 ± 1.03	10.00 ± 0.00	19.29 ± 0.68	21.17 ± 8.28	8.50 ± 7.19	29.50 ± 10.68
Moment $\tilde{N}$	—[e]	—	—	21.56 ± 8.65	—	—

[a] No. distinct individuals captured in samples.
[b] Schnabel (1938).
[c] Estimate ± SE.
[d] Burnham and Overton (1978).
[e] The condition $3f_1f_3 > f_2^2$ is not satisfied, so $\hat{N} = \tilde{N}$.

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PROPOSED MOMENT ESTIMATOR

Assume that the true population size is N and there are t trapping samples. The heterogeneity model assumes that the jth animal has the capture probability p_j, which is constant over trapping samples, and $p_1, p_2, \ldots, p_N$ is a random sample from an arbitrary, unknown distribution function. Under this model, the capture frequencies $(f_1, f_2, \ldots, f_t)$, where f_k is the number of animals captured exactly k times in the t trapping samples, contains all the information for estimating the population size. For example, the jackknife estimator is a linear combination of capture frequencies.

When t is not too small (≥ 5) and most capture probabilities are relatively small, Chao (1987) demonstrated that if most animals are captured only 1–2 times in the samples, then a moment estimator of the population size is obtained as $\hat{N} = S + f_1^2/(2f_2)$, where S is the number of distinct animals captured in the t samples. Also, if f_1, f_2, and f_3 further satisfy the conditions that $tf_1 > 2f_2$, $tf_2 > 3f_3$, and $3f_1f_3 > 2f_2^2$, then a modified moment estimator is $\tilde{N} = S + [f_1^2/(2f_2)]\,[1 - 2f_2/(tf_1)]/[1 - 3f_3/(tf_2)]$. Otherwise, $\tilde{N} = \hat{N}$. All the derivation details are given in Chao (1987). It is clear that $\tilde{N} \geq \hat{N}$.

Both $\hat{N}$ and $\tilde{N}$ are referred to as moment estimators because they are obtained as lower bounds of N subject to some moment constraints. Note that for $\hat{N}$ or $\tilde{N}$, only function of the first 2 or 3 frequency counts are used to predict the number of uncaptured animals, f_0. Intuitively, those animals with small capture probabilities are likely to be uncaptured (i.e., in the frequency f_0) or captured very few times. Thus, it seems reasonable that f_1, f_2, and f_3 would contain most of the information about f_0.

In practical applications, a confidence interval of the population size is more useful than a point estimate. To construct confidence intervals, the following variance estimators are used:

$$\widehat{\text{var}}\ \hat{N} = f_2[0.25(f_1/f_2)^4 + (f_1/f_2)^3 + 0.5(f_1/f_2)^2], \quad \text{and}$$

$$\widehat{\text{var}}\ \tilde{N} = f_2[0.25A^2(f_1/f_2)^4 + A^2(f_1/f_2)^3 + 0.5A(f_1/f_2)^2],$$

where

$$A = [1 - 2f_2/(tf_1)]/[1 - 3f_3/(tf_2)].$$

Thus, a 95% confidence interval based on $\hat{N}$ is obtained as $[S + (\hat{N} - S)/C,\ S + (\hat{N} - S)C]$ where $C = \exp\{1.96[\log(1 + (\widehat{\text{var}}\ \hat{N})/(\hat{N} - S)^2)]^{1/2}\}$. Similarly, one can construct confidence intervals based on $\tilde{N}$.

APPLICATIONS TO REAL DATA SETS

Striped Skunk Data

Greenwood et al. (1985) conducted a live-trapping capture–recapture experiment from a skunk population of known size. They calculated 10 estimators under various models and found that the (first order) jackknife estimator (Table

Table 2. Comparison of 6 population size estimators for eastern cottontails (Edwards and Eberhardt 1967).

Capture frequencies	1961 (18 trap-days)	1963 (8 trap-days)
f_0	59	61
f_1	43	36
f_2	16	15
f_3	8	13
f_4	6	3
f_5		1
f_6	2	1
f_7	1	
S[a]	76	69
Known N	135	130
Geometric (1)[b]	136	151
Geometric (2)[b]	164	150
Schnabel[c]	85 ± 10.5[d]	86 ± 11.0
Jackknife[e]	159 ± 21.9	130 ± 33.8
Moment $\hat{N}$	135 ± 24.0	112 ± 19.4
Moment $\tilde{N}$	136 ± 25.1	126 ± 25.3

[a] No. distinct individuals captured in samples.
[b] Edwards and Eberhardt (1967).
[c] Schnabel (1938).
[d] Estimate ± SE.
[e] Burnham and Overton (1978).

1) gave the best results of all methods evaluated based on 2 comparison criteria. From their data I calculated the moment estimates $\hat{N}$ and $\tilde{N}$ (Table 1). In this case, $\hat{N} = \tilde{N}$ except for females in 1978; therefore, the comparison will be mainly focused on $\hat{N}$.

In 1977, a large portion (≥77%) of the skunks were captured in each data set and the jackknife estimator is accurate. Almost all estimation methods and the moment estimator agree favorably for these data. However, for 1978 the mean capture probability was relatively small and most skunks were caught 1–2 times. For 1978, the moment estimator appears reliable because its bias is relatively small, although the precision is low. The increase in standard error seems unavoidable because of the relatively low capture rates. All the other approaches are biased low.

Greenwood et al. (1985) compared estimators based on mean relative error and median standardized difference. The proposed $\hat{N}$ has a smaller mean relative error (10%) and smaller median standardized difference (0.31) than the 14% and 0.93 values of the jackknife estimator. Thus, using these 2 criteria, the moment estimator is better than the jackknife estimator.

Eastern Cottontail Data

Edwards and Eberhardt (1967) used 2 data sets to illustrate the performance of various estimators. One data set was obtained in 1961 by livetrapping a confined eastern cottontail population for 18 consecutive days and the other was a field record of 8 trapping days obtained in 1963 (Table 2). Although the true population size is unknown for 1963 data, these authors conducted a drive-census and determined the estimated population size was 130 using the Lincoln–Petersen estimator.

Table 3. Comparison of 4 population size estimators for eastern chipmunks (Mares et al. 1981).

Capture frequencies	Data (13 trap-days)
f_0	10
f_1	14
f_2	13
f_3	18
f_4	12
f_5	7
f_6	5
f_7	1
f_8	1
S[a]	72
Known N	82
Schnabel[b]	72.3 ± 5.75[c]
Jackknife[d]	84.9 ± 4.88
Moment $\hat{N}$	79.5 ± 5.31
Moment $\tilde{N}$	81.5 ± 6.50

[a] No. distinct individuals captured in samples.
[b] Schnabel (1938).
[c] Estimate ± SE.
[d] Burnham and Overton (1978).

Edwards and Eberhardt (1967) suggested fitting the capture frequencies by a geometric series and obtained 2 estimates for each data set by different estimation procedures (Table 2). Using their data, I compared $\hat{N}$, $\tilde{N}$, jackknife, and Schnabel estimates (Table 2).

As expected, the Schnabel estimator severely underestimates and the 2 geometric estimators consistently overestimate the true population size. This agrees with the finding of Carothers (1973) and Greenwood et al. (1985). As noted by Seber (1986:275) there is sufficient evidence from the literature to show that models such as geometric or negative binomial are inappropriate. The jackknife and the moment estimates seem reasonable for these data sets. For the 1961 data, Burnham and Overton (1978) suggested using the third-order jackknife estimate of 159. They further provided an improved, interpolated jackknife estimate of 142 but these estimates are worse than the moment estimate $\hat{N}$ or $\tilde{N}$. For the 1963 data, the jackknife method works well, and the proposed $\hat{N}$ is biased low probably because the value of f_3 is relatively

Table 4. Comparison of the jackknife and moment estimators for Carothers (1973) taxicab data (5 trap-days, true value N = 420).

Sampling scheme[a]	Data subset	Capture frequencies f_1	f_2	f_3	f_4	Jackknife method Estimate	SE	95% CI	Proposed method $\hat{N}$	$\tilde{N}$	SE ($\hat{N}$)	95% CI
A	α a	65	12			192	19	155–299	253	—[b]	68	162–444
	b	73	8			217	21	176–258	414	—	142	230–825
	c	75	7			223	21	182–264	484	—	179	256–1,077
	d	109	24	3		325	26	274–376	384	—	71	279–566
	e	112	28	2		332	26	281–383	366	—	54	274–523
	f	117	24	4		350	27	297–403	430	436	80	311–635
	g	135	42	9	1	407	29	350–464	404	405	52	323–533
B	α a	78	5			233	22	190–276	691	—	306	323–1,626
	b	67	9			199	20	160–238	325	—	104	190–624
	c	71	7	1		213	21	172–254	439	457	162	234–914
	d	112	22		2	333	26	282–384	421	—	83	299–635
	e	106	28	3		315	25	266–364	338	—	56	254–481
	f	102	26	3		303	27	250–356	331	—	57	246–479
	g	116	48	6	2	346	20	207–385	312	—	35	259–399

[a] Scheme A designed for equal catchability, scheme B for heterogenous catchability.
[b] The condition $3f_1f_3 > 2f_2^2$ is not satisfied, so $\tilde{N} = \hat{N}$.

large. However, the proposed $\tilde{N}$ is comparable to the jackknife result.

Eastern Chipmunk Data

Mares et al. (1981) released 85 chipmunks for a capture–recapture experiment. During the 13-trap-day period, 3 chipmunks died and were not included in the frequency data (Table 3). These authors compared the mean-Petersen, Schnabel, and Schumacher–Eschmeyer methods and showed that all the results underestimated the true population size. The experiment was designed properly to satisfy all the assumptions except for equal catchability. Thus, the heterogeneity model should be the most appropriate model for these data. I compared the jackknife, $\hat{N}$, $\tilde{N}$, and Schnabel estimates (Table 3). The jackknife and the moment estimator work better than the 3 methods considered by Mares et al. (1981). The moment estimator $\tilde{N}$ is closest to the true value of 82. This example shows that even if the data information is increased to $f_3, f_4, \ldots, f_t$, $\hat{N}$ and $\tilde{N}$ may still work in some cases if a large portion of animals are captured.

Taxicab Data

Carothers (1973) regarded each taxicab in the city of Edinburgh as an animal and captured or recaptured it by recording its registration number. Data sets obtained from the first 5 trapping days (Table 4) were considered. Two sampling methods were used: various sampling times and locations were selected to ensure equal catchability (scheme A), and the same sampling time and point were chosen on all trapping days (scheme B) to ensure heterogeneity in catchability.

Applying various estimators to the resulting data, Carothers (1973) found that most of the estimators based on the equal-catchability assumption were negatively biased. I compared the (non-interpolated) jackknife point and interval estimates, the moment estimates $\hat{N}$ and $\tilde{N}$, and the 95% confidence intervals based on $\hat{N}$ (Table 4). The jackknife method underestimates the population size and only 1 of the 14 95% confidence intervals covers the true parameter. Because the information for each data subset is primarily concentrated on f_1 and f_2, the moment estimators usually produce more reliable results and, on average, are closer to the true value of N. There are only 3 cases for which $\hat{N} \neq \tilde{N}$, because f_3's are usually small and the condition $3f_1f_3 > 2f_2^2$ is not satisfied. With such low capture rates and small numbers of total captures, it seems impossible to obtain quite precise results. The proposed intervals are wider than the jackknife intervals, but 13 of 14 intervals correctly include the true parameter.

SIMULATION COMPARISONS

The following discusses the behavior of the jackknife and moment estimators during a Monte Carlo simulation. The bias, standard error, and confidence interval for each method were in-

Table 5. Simulation comparison of the jackknife and proposed estimator (N = 400, 200 simulations, and nominal probability for CI = 95%).

Trial	E(p)[a]	SE(p)	Capture probability	n trapping samples	Theoretical capture frequencies				Jackknife method			Proposed method $\hat{N}$		
					Ef_1	Ef_2	Ef_3	Ef_4	Estimate	SE	% coverage	Estimate	SE	% coverage
1	0.05	0.022	$p_i \sim 0.1 \times$ beta(2, 2)	5	78.3	9.8	0.7	0.0	229	21.5		445	167.2	97.0
				10	116.5	31.4	5.8	0.8	416	43.3	83.0	374	74.5	98.0
2	0.05	0.029	$p_i \sim$ U(0, 0.1)	5	76.2	10.6	0.8	0.0	227	21.4		402	143.3	97.0
				10	110.1	32.6	6.7	1.0	388	40.5	80.5	340	65.6	96.5
3	0.05	0.039	$p_i \sim 0.2 \times$ beta(1, 3)	5	72.4	11.7	1.3	0.1	208	20.5		351	124.9	94.5
				10	100.8	32.5	8.5	1.8	352	37.9	62.5	308	62.1	78.5
4	0.05	0.0433	$p_i = 0.025, i = 1, 300$	5	70.5	12.2	1.5	0.1	208	20.5		306	100.3	86.0
			$p_i = 0.125, i = 301, 400$	10	97.3	31.1	9.7	2.3	350	38.1	58.0	299	59.0	75.5
5	0.05	0.0520	$p_i = 0.02, i = 1, 300$	5	66.0	13.6	2.1	0.2	194	19.9		253	78.0	68.5
			$p_i = 0.14, i = 301, 400$	10	86.1	31.0	11.7	3.3	310	34.1	40.0	260	50.9	46.5
6	0.1	0.029	$p_i \sim$ U(0.05, 0.15)	5	127.2	30.1	3.9	0.3	379	27.8	87.5	442	89.7	97.5
				10	147.6	74.9	24.7	5.7	478	33.4	35.5	403	48.6	100.0
7	0.1	0.045	$p_i \sim 0.2 \times$ beta(2, 2)	5	121.4	31.4	4.7	0.4	362	27.1	71.0	411	83.6	99.0
				10	136.5	72.2	26.9	7.4	448	31.5	72.0	378	46.1	100.0
8	0.1	0.058	$p_i \sim$ U(0, 0.2)	5	114.9	33.0	5.7	0.5	346	26.5	46.5	364	70.8	97.0
				10	123.3	69.6	29.3	9.2	404	27.3	89.0	343	40.4	94.0
9	0.1	0.066	$p_i \sim$ beta(2, 18)	5	112.6	32.2	6.4	0.8	335	26.1	29.0	356	70.9	96.5
				10	124.8	64.8	27.6	10.1	424	43.2	87.0	356	45.0	98.0
10	0.1	0.078	$p_i \sim 0.4 \times$ beta(1, 3)	5	104.9	33.6	7.7	1.1	307	24.9	5.0	316	63.7	86.0
				10	110.7	61.0	29.6	12.2	381	29.2	64.5	321	41.2	76.5
11	0.1	0.087	$p_i = 0.05, i = 1, 300$	5	100.6	32.8	9.1	1.5	306	24.8	5.0	303	58.1	80.0
			$p_i = 0.25, i = 301, 400$	10	113.3	50.5	28.2	14.9	423	37.1	73.0	344	47.0	92.5
12	0.1	0.105	$p_i = 0.03, i = 1, 150$	5	88.0	33.6	11.6	2.3	272	23.1	6.0	255	47.7	35.0
			$p_i = 0.05, i = 151, 300$	10	96.2	41.3	28.1	18.1	385	36.2	69.5	310	44.5	72.0
			$p_i = 0.26, i = 301, 350$											
			$p_i = 0.30, i = 351, 400$											

[a] $\bar{x}$ capture probability.

vestigated. I generally followed the simulation procedure used in Otis et al. (1978), and only considered populations with small mean capture probability (0.05 and 0.1) (E[p]). All computations were done on a CDC Cyber-840 computer at National Tsing Hua University.

The true population size was fixed at 400. For $E(p) = 0.05$ and 0.1, 5 and 7 populations with varying degrees of heterogeneity were considered, respectively (Table 5). Three classes of distributions were selected to model the capture probability: uniform, beta, and a realization of discrete distributions. For each given population, 200 data sets were generated with $t = 5$ and 10. Then, for each generated data set the point estimate, its standard error, and the corresponding confidence interval were computed for the (non-interpolated) jackknife and moment estimator $\hat{N}$. In the calculation of the jackknife estimates, I followed the testing procedure in Burnham and Overton (1978, 1979) to select an appropriate order of the jackknife estimator up to the fifth order. Finally, these 200 estimates and standard errors were averaged and the coverage probabilities were estimated. The theoretical values of Ef_i, for i = 1 to 4, are also listed for each case (Table 5).

Generally, the jackknife estimator has considerably smaller standard error and this error increases when t increases from 5 to 10. The reverse is true for the moment estimator. When $t = 10$, relatively more individuals are captured >2 times, and the jackknife estimator is evidently superior to the moment estimator. However, when $t = 5$, the moment estimates in most cases are closer to the true population size, especially when $E(p) = 0.05$. Note that in trials 11 and 12 (Table 5), the moment estimator $\hat{N}$ for both cases $t = 5$ and $t = 10$ is less satisfactory because the values of f_3 in those trials are relatively large and thus are non-negligible.

The coverage probabilities of the jackknife confidence intervals are usually much less than the nominal level of 0.95. When $t = 5$ and $E(p) = 0.05$, none of the 200 intervals for each trial cover the true value. The proposed confidence interval in some cases is too conservative, but it behaves better in maintaining the anticipated probabilities, although the confidence interval lengths are clearly wider.

Finally, it should be noted that if the degree of heterogeneity of the population is increased, relatively more animals would be captured more times and the moment estimator will have a severe negative bias, as shown in trials 11 and 12. This becomes a serious limitation of the proposed method.

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