MARK-RECAPTURE MODELS -CLOSED POPULATIONS
NOTES FOR W478 LAB

<u>Reading</u>

Chapters 1,7 in, White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, N.M.

Chapters 2.1,2.2,2.4-2.6 in, Krebs, C. J. 1989. Ecological Methodology.Harper Collins, New York.

ESTIMATION OF DENSITY OR POPULATION SIZE

Absolute density- the number of organisms per unit area or volume,
Relative density- the density of one population relative to that of another population.

from Krebs, C. J. 1989. Ecological Methodology. Harper Collins, New York.

MODELS FOR CLOSED POPULATIONS

Closure- The size of the population is constant over the period of investigation: no recruitment (birth or immigration) or losses (death or emigration) occur.

Geographic closure- Closure by boundary, animals do not move in or out of the area that is being trapped.

Demographic closure- Closure to birth, immigration, death, and emigration.

$$\hat{N} = \frac{n_1 n_2}{m_2}$$

<u>Lincoln-Petersen estimator</u>:
there n_1= no. caught on the first occasion, n_2=no. caught on the second trapping occasion, and m_2= no. of marked animals recaptured on the second occasion.

$$\hat{N}_c = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1$$

<u>Unbiased estimator for L-P</u>:
(The c refers to Chapman's estimator)
Confidence intervals for the L-P estimator can be calculated in a variety of ways. One approximation is:

$$\hat{Var}(\hat{N}_c) = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)}$$

(p. 10 in Pollock et al. 1990. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107:1-97). See Krebs (1989) for a discussion of other approaches to estimating confidence intervals for L-P estimators

A more general approach:

$$\hat{N} = \frac{n}{\mathbf{p}}$$

Where n=no. animals caught, and ***p***=probability of capture.

In general:
p_{ij}= capture probability of individual i on capture occasion j.

Sources of variation in capture probabilities
Time- Probability of capture differs between capture periods.

Behavior- Probability of capture varies as a function of capture history. After initial capture, probability of capture may increase (trap happy response) or decrease (trap shy response).

Heterogenity- Probability of capture differs between individuals in the population.

Assumptions of Mark-Recapture models for closed pops
1. Population closed
2. Animals do not lose marks
3. All marks are noted and recorded correctly

Additional assumptions (model dependent)
4. No variation in capture probabilities over time
5. No variation in capture probabilities as a function of capture history (behavior)
6. No variation in capture probabilities between individuals (heterogeneity)

L-P requires that assumptions 1-3, 5, 6 be met
Other models may be more or less restrictive. For more information on other mark-recapture models for closed populations, see White et al. 1982, Ch.3.

Schnabel method- Extension of the L-P model to more than 2 capture occasions.

C_t= Total number of individuals caught in sample t.

R_t= Number of marked individuals caught at time t.

U_t= Number of individuals marked for the first time and released in sample t.

M_t= Number of marked individuals in the population just before the tth sample is taken.

The population size is estimated as:

$$\hat{N} = \frac{\sum(C_t M_t)}{\sum R_t}$$

If the fraction of the population that is caught in each sample (C_t/N) and the fraction of the total population that is marked (M_t/N) are always less than 0.1 then a better estimate is:

$$\hat{N} = \frac{\sum(C_t M_t)}{(\sum R_t) + 1}$$

The variance is calculated on the reciprocal of N:

$$Var(1 / \hat{N}) = \frac{\sum R_t}{(\sum C_t M_t)^2}$$

and the standard error is:

$$se\,(1 / \hat{N}) = \sqrt{Var(1 / \hat{N})}$$

To obtain a confidence interval, use the standard error obtained above and the appropriate *t*-value from a *t*-table:

$$1 / \hat{N} \pm t_{\alpha}\, se$$

Use t-1 for the degrees of freedom in the *t*-table, where t is the number of trapping occasions.

Schumacher-Eschmeyer Method

The Schumacher-Eschmeyer method can also be used with more than 2 capture occasions. The assumptions are the same as the Schnabel method and the approach is covered by Krebs (1989).

Program CAPTURE

Program CAPTURE is the most general approach to analysis of mark-recapture data for closed populations. The program calculates population estimates using a variety of different models and then chooses the one that "fits" best. This approach is excellent if population size and probability of capture are both high.

Detecting violations of the assumptions of mark-recapture models

The schnabel method is an extension of the L-P approach and therefore has the same assumptions. The advantage to using multiple capture occasions is two-fold.

1. The estimate is based on more captures and therefore is more precise.
2. Assumptions of equal catchability can be tested.

There are a number of tests that have been developed to test the assumption of equal catchability. One of the most efficient tests of equal catchability is the **Zero-truncated Poisson Test**. This test can be used if there are four or more trapping occasions and if the period between trapping occasions is short enough to ensure little or no mortality. Krebs (1989, p. 47) provides a detailed explanation of the test with an example.

The test is based on an analysis of the capture frequency of animals in the population. Capture frequency is the number of times that an animal was caught during the sampling period. The capture frequency for each animal in the population is tabulated and then the distribution of capture frequencies for the population is tallied. For example, using the data below, there were 10 animals that were captured on 1 occasion, 7 on 2 occasions, 2 on 3 occasions, and 0 on 4 occasions. Thus the observed capture frequencies are: f_1=12, f_2=5, f_3=1, f_4=1. These observed frequencies are then compared to frequencies expected from a random sampling of the population. The expected frequencies can be generated using a binomial or a Poisson distribution. I give the formulas for calculating the expected frequencies below. See Seber (1982, p. 169) for the solution using the binomial distribution.

$$\bar{x} = \frac{\sum f_x x}{\sum f_x}$$

Calculate the mean of the observed data:
Where x = number of times captured,and f_x = number of animals caught x times.

$$\bar{x} = \frac{m}{1 - e^{-m}}$$

$$E(f_x) = \sum f_x \left(\frac{e^{-m}}{1 - e^{-m}} \frac{m^x}{x!}\right)$$

Solve for m using the equation (this must be done iteratively):
Calculate the expected value using the formula for a Poisson distribution:
Test for goodness of fit using a χ^2 test.

Data and summary statistics for mark-recapture studies

Animal (i)	Capture occasion (j or t) 1	2	3	4=t	F_i
i=1	1	0	0	0	1
2	1	0	0	0	1
3	1	0	0	0	1
4	1	1	0	0	2
5	1	0	1	0	2
6	1	0	1	1	3
7	1	1	1	1	4
8	0	1	0	0	1
9	0	1	0	0	1
10	0	1	0	0	1
11	0	1	1	0	2
12	0	1	0	1	2
13	0	0	1	0	1
14	0	0	1	0	1
15	0	0	1	0	1
16	0	0	1	1	2
17	0	0	0	1	1
18	0	0	0	1	1
19	0	0	0	1	1

Animals caught	n_j =	7	7	8	7	$n_.$=29
Total caught	M_j =	0	7	12	16	M_{t+1}=19 $M_.$=35
Newly caught	u_j =	7	5	4	3	
Frequencies	F_j =	12	5	1	1	
Other statistics						
recaptures	m_j =	-	2	4	4	$m_.$=10

Using the capture matrix above complete the following exercises:

1. Calculate N(HAT) and 95% confidence intervals using the Schnabel method.

2. Plot the proportion marked in capture occasion *t* versus the number of animals previously marked.

3. Test for equal probability of capture using the Zero-Truncated Poisson Test.

4. Calculate N(HAT) and 95% confidence intervals using the L-P method. Use the first two capture occasions as the mark period and the second two as the recapture period.

Eliminating variation due to time, behavior, and heterogenity
(pages 163-164 in White et al. 1983)
1. Time- Expend equal effort each time, when weather conditions are as constant as possible.

2. Behavior- Use different methods of capture if a trap response is suspected.

3. Heterogenity-
    a. Trap accessibility- > 4 traps/home range, move traps, 2 traps/station.
    b. Social interactions- increase trap density, stratify data.

Sample size considerations (pages 164-168 in White et al. 1982)
Here sample size refers to the number of animals captured and recaptured, not to the number of plots to be sampled. The factors that influence the expected number of captures are:
1. Grid size- White et al. 1983 recommend r+c>25 (r=# rows, c=# columns of grid) for estimation of density. For spacing they recommend s#W/2 where W is the average width of the home range.
2. Capture probability- >0.3 for N<100. See Skalski and Robson 1992 pp. 78-94.
3. Number of trapping occasions- a minimum of 5.
4. Population size- Generally the estimators work best if N>100. White et al. recommend adjusting grid size to increase the size of the population being estimated. If probability of capture is high, good estimates can be achieved for smaller populations.

L-P may be more efficient and accurate than CAPTURE when n is small (50-100) see Menkens and Anderson 1988.

Some references on mark-recapture techniques for closed populations
Krebs, C. J. 1989. Ecological Methodology. Harper Collins, New York.

Menkens, G. E., and S. H. Anderson. 1988. Estimation of small mammal population size. Ecology 69:1952-1959.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed populations. Wildl. Monogr. 62:1-135.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. Griffen, London, England.

Skalski, J. R., and D. S. Robson. 1992. Techniques for wildlife investigations: Design and analysis of capture data. Academic Press, San Diego.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratories. LA-8787-NERP, Los Alamos, N.M. 235pp.

CAPTURE-RECAPTURE MODELS FOR OPEN POPULATIONS
Reading Krebs Ch 2.3

Additional reading on open population models

Krebs, C. J. 1989. Ecological Methodology. Harper Collins, New York.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E.Hines. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107:1-97

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second ed. MacMillan, New York, N. Y. 645 pp.

The Jolly-Seber Model and analysis
Consider a multiple capture-recapture survey in which there is the possibility of a) a gain in population numbers through recruitment or immigration, or b) a loss in population numbers through death or permanent emigration.

<u>Assumptions of the Jolly-Seber method</u>

1. p_t = probability of capture in the t^{th} sample is the same for all animals (marked and unmarked).

2. Φ_t = probability of survival from t to t+1 is the same for all marked animals.

3. No errors in identification of individuals, no tag losses.

4. Sampling is instantaneous, i.e. the population size does not change during the sampling event.

Note:
-Capture probability can vary from one period to the next.

- (1-Φ) is the probability of death and/or permanent emigration. This means that birth and immigration, and emigration and death are completely confounded.

- Differences in capture probabilities between marked and unmarked animals only affects the estimates of population size, not estimates of survival.

Jolly-Seber model

Unknown parameters

1. p_t = capture probability at time t.

2. Φ_t = survival probability at time t to t+1.

3. N_t = population size just prior to t.

4. M_t = number of marked animals at risk of capture just prior to t.

5. B_t = number of new animals gained between t and t+1.

Data and summary statistics

1. n_t = sample size at t.

2. m_t = number of marked animals caught at t.

3. s_t = number of marked animals released at t

4. R_t = number of marked animals released at t and later recaptured.

5. Z_t = number of marked animals not caught in the i^{th} sample but later recaptured.

6. k = number of sampling occasions.

Notes:

a) $m_1 = Z_1 = 0$
R_k and Z_k are undefined.
$M_1 = 0$

b) If an animal is caught, then leaves the study area for several trapping occasions, then returns and is recaptured, the model assumes that the animal has been at risk the entire time.

c) If $s_t = 0$ or $R_t = 0$ then estimates of M_t do not exist. This is analogous to a L-P estimator with no recaptures on the second occasion.

d) Data are often displayed in a matrix (Method B). (see Krebs 1989)

Hypothetical x-matrix

	Trapping occasion			
Animal	1	2	3	4
1	1	1	1	0
2	1	0	1	0
3	1	0	0	1
4	1	0	0	0
5	1	1	1	1
6	1	0	1	0
7	1	1	0	0
8	1	1	0	0
9	1	0	0	1
10	1	1	1	0
11	0	1	1	0
12	0	1	0	1
13	0	1	0	0
14	0	0	1	0
15	0	0	1	1
16	0	0	1	0
17	0	0	1	0
18	0	0	0	1
19	0	0	0	1
20	0	0	0	1

	Trapping occasion			
Summary statistics	1	2	3	4
Total sample size n_t	10	8	10	8
No. marked animals caught m_t	0	5	6	5
No. marked animals released s_t	10	8	10	8
No. released and later recaptured R_t	9	5	2	-
No. marked animals not caught but later recaptured Z_t	0	4	3	-

1. Estimation of M_t (number of marked animals available at risk just prior to t.
A Lincoln-Petersen type estimator is assumed:

$$\frac{Z_t}{\hat{M}_t - m_t} = \frac{R_t}{s_t}$$

Interpretation of equation:

No. marks not caught at t		No. marks released at t
<u>but later recaptured</u>	=	<u>and later recaptured</u>
No. marks not caught at t		No. marks released at t

Solving for M_t:

$$\hat{M}_t = \frac{s_t Z_t}{R_t} + m_t$$

The unbiased version is:

$$\hat{M}_t = \frac{(s_t + 1)\hat{M}_t}{(R_t + 1)} + m_t$$

2. Estimation of N_t (population size just prior to trapping occasion at t).
Once you have calculated M_t, follow the Lincoln-Petersen index,

$$\frac{\hat{M}_t}{\hat{N}_t} = \frac{m_t}{n_t}$$

Rearranging

$$\hat{N}_t = \frac{n_t \hat{M}_t}{m_t}$$

The unbiased version is:

$$\hat{N}_t = \frac{(n_t + 1)\hat{M}_t}{(m_t + 1)}$$

3. Estimation of Φ_t (survival of marked animals):

$$\hat{\phi}_t = \frac{\hat{M}_{t+1}}{\hat{M}_t + (s_t - m_t)}$$

or $\dfrac{\text{Estimated no. of marks alive at t+1}}{\text{Estimated no. of marks alive just after t}}$

4. Estimation of p_t the probability of capture at time t. It is assumed that p_t is the same for all animals:

$$\hat{p}_t = \frac{n_t}{\hat{N}_t}$$

or no. caught on occasion t / estimated pop. size on occasion t

5. Estimation of B_t

$$\hat{B}_t = \hat{N}_{t+1} - \hat{\Phi}_t [(\hat{N}_t - (n_t - s_t))]$$

or: estimated pop. size at t+1 - estimated no. surviving from t to t+1.

This assumes that survival is the same for all animals.