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Lecture 06 – Multinomials and CMR Models for closed populations

Readings

> Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press. San Diego, California.

Other resources

> Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monograph 62. 135pp.

> Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107. 97pp.

> 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, Rep. LA-8787-NERP. 235pp. – Chapter 1, Chapter 8

Multinomial Distribution and Likelihoods

> A fundamental appreciation for the **multinomial coefficient**, **multinomial distribution**, **and multinomial likelihood** is of great importance to understanding and analyzing capture-mark-recapture data. The multinomial coefficient is an extension of the binomial coefficient with more than two possible mutually exclusive outcomes. As the binomial coefficient was introduced by way of coin tossing, the multinomial coefficient is nearly always introduced by way of die tossing. The multinomial coefficient or the number of possible outcomes for die tossing is written:

$$\begin{pmatrix} n \\ y_1\, y_2\, y_3\, y_4\, y_5\, y_6 \end{pmatrix} = \frac{n!}{y_1!\,y_2!\,y_3!\,y_4!\,y_5!\,y_6!} = \frac{n!}{\prod_{i=1}^{6} y_i!}\,.$$

1. Dependency among counts

> One property of multinomial data is that there is a dependency among the counts. For example, if a die is thrown and it is not a 1, 2, 3, 4, or 5, then it must be a 6. Thus in the table below if we know any 5 of the variables and the total number of trials (tosses) we know the 6th. This dependency is a characteristic of the binomial coefficient as well. If we know number of trials (n) and the number of heads (y), we then know the number of tails ($n - y$).

Face	Number	Variable
1	10	y_1
2	11	y_2
3	13	y_3
4	9	y_4
5	8	y_5
6	9	y_6
TOTAL	60	n

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2. Probability distribution function

We can also write the probability an outcome or series of outcomes from the multinomial in the form of a probability statement:

$$f(y_i \mid n\, p_i) = \binom{n}{y_i} p_1\, p_2\, p_3\, p_4\, p_5\, p_6$$

Note that $\sum p_i = 1$. Why?

For example, the probability of rolling a fair die (p_i = 1/6) six times (n) and turning up each face only once (n_i = 1) is written:

$$f(1,1,1,1,1,1 \mid 6\ 1/6,1/6,1/6,1/6,1/6,1/6) = \frac{6!}{1!\cdot 1!\cdot 1!\cdot 1!\cdot 1!\cdot 1!}\cdot\frac{1}{6}\cdot\frac{1}{6}\cdot\frac{1}{6}\cdot\frac{1}{6}\cdot\frac{1}{6}\cdot\frac{1}{6} = 0.01543$$

Table 1. Vertical file.	
Tag No.	Date
211	2/1/1991
211	3/2/1993
212	2/6/1991
213	3/1/1993
214	3/1/1991
214	2/10/1993
.	.
.	.
.	.

Another example, the probability of rolling 2 – 2s , 3 – 3s, and 1 – 4 is:

$$f(0,2,3,1,0,0 \mid 6\ 1/6,1/6,1/6,1/6,1/6,1/6) = \frac{6!}{(0!)(2!)(3!)(1!)(0!)(0!)}\left(\frac{1}{6}\right)\left(\frac{1}{6}\right)\left(\frac{1}{6}\right)\left(\frac{1}{6}\right)\left(\frac{1}{6}\right)\left(\frac{1}{6}\right) = 0.001286$$

3. Likelihood

As you might have expected, the likelihood of the multinomial is of greater interest to us, since in ecology we frequently have data (n, $y_{i...m}$) and are seeking to determine the model (p_i). The likelihood for our example with the die is:

$$\mathcal{L}(p_i \mid n\, y_i) = \binom{n}{y_i} p_1^{y_1}\, p_2^{y_2}\, p_3^{y_3}\, p_4^{y_4}\, p_5^{y_5}\, p_6^{y_6}$$

This likelihood has all of the same properties we discussed for the binomial case. so as you might have expected, we are interested in the log-likelihood:

$$\ln(\mathcal{L}(p_i \mid n\, y_i) = \ln\binom{n}{y} + y_1 \ln(p_1) + y_2 \ln(p_2) + y_3 \ln(p_3) + \ldots y_m \ln(p_m)$$

$$= \ln\binom{n}{y} + \sum_{i=1}^{m} y_i \ln(p_i)$$

which is frequently abbreviated as

$$\ln(\mathcal{L}(p_i \mid n\, y_i) = \ln(C) + \sum_{i=1}^{m}\left(y_i \ln(p_i)\right)$$

The multinomial coefficient like the binomial coefficient can be ignored so what we end up with is:

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$$\ln(\mathcal{L}(p_i \mid n \ y_i)) = \sum_{i=1}^{m} \left(y_i \ln(p_i) \right)$$

$$= \sum \left(data \times \ln(probability) \right)$$

4.   Capture histories & multinomials

Typically the procedure that is followed in CMR studies is to capture a sample of animals, mark them so that they are uniquely identifiable, release them, and record either recoveries of dead animals or recaptures and observations (resightings) of live animals. These data may be recorded in the form of a "vertical file" that may include ancillary information (i.e., covariates) like Table 1.

These observations are typically converted to the form of a capture-history matrix where each row represents an individual and each column represents a sampling occasion. On each occasion each individual is assigned a '1' if encountered (captured) or a '0' if not encountered. Ultimately for the closed population estimators discussed in this section these are converted to 'LLLL' data. For example, in a live-release study of with one initial capture and three sampling occasions, the capture histories of ten individuals captured and released on occasion 1 might look like Table 2.

For individuals in a population sampled on 3 occasions 8 ($=2^m = 2^3$) possible capture histories. The next table demonstrates how these observations can be summarized by the number of individuals (y_i) characterized by each possible capture history.

These data can be used to estimate a number of useful parameters such as population size, survival, re-sighting and the assumptions we are willing to make.

Table 2. Capture histories.

	Occasion		
Tag No.	1	2	3
211	0	0	1
212	0	0	1
213	0	1	0
214	1	0	0
215	1	0	1
216	1	1	0
217	1	1	1
218	0	0	1

rate depending upon the data

Table 3. Summarized histories.

y_i	Capture History		
1	1	0	0
2	1	0	1
2	1	1	0
1	1	1	1
3	0	0	1
1	0	1	0
0	0	1	1
$N - \sum_{i=1}^{m-1} y_i$	0	0	0

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5. How does all of this relate back to Multinomials and Likelihoods?

Remember the table from the example of the roll of the die.

Face	Number (y_i)
1	10
2	11
3	13
4	9
5	8
6	9
TOTAL	60

The likelihood for such a data set could be constructed as:

$$\sum \left(data \cdot \ln(probability) \right)$$

In CMR studies, each capture history is a possible outcome, analogous to one face of the die (n_i). Our data consist of the number of times each capture history appears (y_i).

y_i	Capture History
3	0 0 1

Each encounter has an associated probability (p_i). For example, the capture history [1 0 1] could be interpreted as:

$Pr\{$Given release at time 1, not recaptured on occasion 2, and captured on occasion 3$\}$

or

$Pr\{R_1|(1\text{-}p_1)\bullet(1\text{-}p_2)\bullet(p_3)\}$,

Thus, we could construct the likelihood for our data of m capture histories of the form:

$$\sum_{i=1}^{m} \left(data \cdot \ln(probability) \right).$$

6. Dependency in the multinomial distribution:

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Because of the numerical dependencies in the multinomial distribution some values necessary for estimating parameters can be determined by subtraction.

How many individuals were never recaptured?

$$\left(R_i - \sum_{j=1}^{m-1} y_{ij} \right)$$

How many were never captured?

$$\left(N. - \sum_{i=1}^{m} R_i \right)$$

Probability of never captured

$$1 - \sum Pr\left\{ \text{capture histories} \right\}$$

Closed Population Recapture Models

CMR techniques have been used to estimate the size of human populations since the mid-1600s. First used in ecology by C.G.J. Petersen to estimate abundance of a fish population in 1896. First used in wildlife science by Lincoln to estimate the abundance of ducks using band-return data in 1930.

The fundamental principle is simple and requires only two sampling occasions. First, a sample of animals (size M - marked) captured from and then marked and released back into the population of interest (size N). Then, another sample of individuals is captured (size C - captured) and the number of individuals marked in C is counted (R - recaptured).

If the second sample was random, the proportion of marked individuals in the second sample reflects the proportion marked in the entire population. Thus, the estimator is based on the proportion:

$$\frac{\hat{N}}{M} = \frac{C}{R}$$

Therefore, the Lincoln-Petersen estimator for N is:

$$\hat{N} = \frac{CM}{R}$$

However, this intuitive estimator tends to be biased and can overestimate population size, especially with small samples. Seber (1982) recommended a different form of the estimator, which is unbiased if $(M + C) \geq N$ and nearly unbiased if $R > 7$:

$$\hat{N} = \frac{(C+1)(M+1)}{R+1} - 1$$

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Think of the classical ball and urn model of Feller (1950). This model is quite different from what is often encountered in the real world in that:

    a. Capture probabilities often vary
       (i.e., animals rarely assort randomly after the first capture).

    b. Closure either demographic or geographic is rarely complete

       1) Demographic closure—no births or deaths
       2) Geographic closure—no emigration or immigration

A large number of researchers and statisticians have contributed to the refinement of these estimators. Otis et al. (1978) provide an extensive treatment of the use of CMR data. His work dealt mainly with examining the sources of variation in capture probabilities. White et al. (1982) is another excellent source of information regarding the analysis of CMR data.

The object of these treatises was the **estimation of population size**, and a fundamental assumption of the approach was population closure. As such survival or recruitment rates were considered nuisance parameters and of little interest.

2. Significant advances of closed models in recent years:

    a. Can be used to examine removal or live-release data.

    b. With more than two sampling occasions, the assumption of constant recapture probability over time can be tested.

    c. Development of MLEs

    d. Heterogeneity of recapture probability can be examined. (i.e., models where capture probability varies among individuals)

    e. Heterogeneity models (i.e., comparisons of groups)

    f. Individuals covariates via link functions

    g. Mixture models – used to model unidentified sources of heterogeneity

3. Lincoln-Peterson Estimator

Despite the weaknesses of this simple estimator it forms the basis for virtually all of the CMR methods.

    a. Key assumptions:

    b. Population is closed – demographically and geographically

    c. Marks are not missed or lost.

    d. Capture probabilities are equal among individuals.

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e. Probability distribution

$$P(n_1, n_2, m_2 \mid N, p_1, p_2) = \frac{N!}{m_2!(n_1 - m_2)!(n_1 - m_2)!(N - n_1 - n_2)!}$$
$$\times (p_1 p_2)^{m_2} (p_1(1-p_2))^{n_1 - m_2} ((1-p_1)p_2)^{n_2 - m_2} ((1-p_1)(1-p_2))^{N-(n_1+n_2)}$$

N	population size	m_2	number marked animals caught in second period
n_1	number caught and marked in first period	p_1	probability of capture in first period
n_2	number caught in second period	p_2	probability of capture during second period

L-P is positively (+) biased and magnitude of bias is inversely related to the sample size.

f. Assumptions
1) Closure – trapping mortality further positively biases the estimate of N
2) Capture probability
   a) Can differ between occasions
   b) Should be equal among individuals
   c) trap happy – negatively biases $\hat{N}$
   d) trap shy – positively biases $\hat{N}$
   e) Tags lost or missed – positively biases $\hat{N}$

4. *K*-sample Capture-Recapture Models

These models differ from the Lincoln-Peterson estimator and Seber's estimator in that they involve more than two sampling occasions

a. Sampling scheme/Data structure
1) Assumptions
   a) Closure – demographic and geographic
   b) Tags are not lost or missed
   c) Capture probabilities are appropriately modeled (the model is correct)
2) Data structure

b. The data consist of capture histories identical to those used in the open models for recovery and recapture data. An encounter history is developed for each uniquely-marked individual consisting of 1s (encounter) or 0s (not encountered) for each potential capture occasion (survey, trapping event, etc.)

5. Modeling approach

These data follow a multinomial distribution:

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$$P(n_i \mid N, p_i) = \frac{N!}{\prod\limits_{i=1}^{K} n_i!} \prod_{i=1}^{K} p_i^{n_i}$$

where n_i and p_i are the number of observations and probability of each capture history. Also, like the open population models, closed populations can be constrained to reduce the number of parameters that are estimated. Additionally, constraints can produce models that estimate the probability of capture for unmarked (p_c) and marked animals (p_r). Thus reducing the total number of parameters estimate from the full 2^K in the general model.

Eight models possible in *K*-Sample Recapture Models.

Model Name	Sources of capture probability variation	Estimated parameters
M_0	Constant capture probability.	N, p
M_t	Temporal variation	N, p_i ($i = 1...K$)
M_b	Behavioral response (trap-happy or trap shy)	N, p_c, p_i
M_h	Individual heterogeneity	N, p_i ($i = 1...N$)
M_{tb}	Temporal and behavioral	N, p_{ci}, p_{ri} ($i = 1...K$)
M_{bh}	Behavioral response and individual heterogeneity	N, p_{ci}, p_{ri} ($i = 1...N$)
M_{th}	Temporal variation and individual heterogeneity	N, p_{ij} ($i = 1...K$) ($j = 1...N$)
M_{tbh}	Temporal variation, behavioral response and individual heterogeneity	N, p_{cij}, p_{rji} ($i = 1...K$) ($j = 1...N$)

Only the first 3 models, M_0, M_t, and M_b, can be directly estimated via the likelihood. For the other 5 models, alternative assumptions and constraints are required. For the model M_{tb}, an MLE can be derived by assuming a relationship between the time-specific capture and recapture probabilities. For models M_h, M_{bh}, and M_{th}, the estimates can be derived under the assumption that capture probabilities these are random samples of size N from an underlying distribution of probabilities, or by using the concept of coverage. However, the finite mixture models described by Pledger (2000) present a better approach based on random effects.

Table 14.1 from Williams et al. 2002

Capture   Probability

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history	M_0	M_t	M_b
111	p^3	$p_1 p_2 p_3$	$p_c p_r^2$
110	$p^2(1\text{-}p)$	$p_1 p_2 (1\text{-}p_3)$	$p_c p_r (1\text{-}p_r)$
101	$p^2(1\text{-}p)$	$p_1 (1\text{-}p_2) p_3$	$p_c p_r (1\text{-}p_r)$
100	$p(1\text{-}p)^2$	$p_1 (1\text{-}p_2)(1\text{-}p_3)$	$p_c (1\text{-}p_r)^2$
011	$p^2(1\text{-}p)$	$(1\text{-}p_1) p_2 p_3$	$(1\text{-}p_c) p_c p_r$
010	$p(1\text{-}p)^2$	$(1\text{-}p_1) p_2 (1\text{-}p_3)$	$(1\text{-}p_c) p_c (1\text{-}p_r)$
001	$p(1\text{-}p)^2$	$(1\text{-}p_1)(1\text{-}p_2) p_3$	$(1\text{-}p_c)^2 p_c$
000	$(1\text{-}p)^3$	$(1\text{-}p_1)(1\text{-}p_2)(1\text{-}p_3)$	$(1\text{-}p_c)^3$

6. Estimating population size

   a. Constant capture probability – Model M_0

   Because all of the capture probabilities are constrained to be equal, the probability distribution reduces to:

   $$P(x_w \mid N, p) = \frac{N!}{\left[\prod_{w=1}^{W} x_w! \right] (N - M_{K+1})!} \, p^{n.} (1-p)^{KN-n.}$$

   where $n_.$ is the total number of captures and M_{K+1} is the total number of unmarked animals captured.

   b. Temporal variation in capture probability – Model M_t

   This model can be thought of as an extension of the Lincoln-Peterson index with the benefit of the additional information from multiple sampling occasions. The number of estimated parameters (N, $p_1...p_K$) is equal to $K+1$, one more than the number of sampling occasions. The probability distribution of this model is:

   $$P(x_w \mid N, p_i) = \frac{N!}{\left[\prod_{w=1}^{W} x_w! \right] (N - M_{K+1})!} \prod_{i=1}^{K} p_i^{n_i} (1-p_i)^{N-n_i} \ .$$

   Note that when $K = 2$, it can be shown that this is the Lincoln-Peterson estimator.

   The population size can be estimated by maximizing with respect to N, or using:

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$$1 - \frac{M_{K+1}}{N} = \prod_{i=1}^{K}\left(1 - \frac{n_i}{N}\right)$$

Darroch (1958), which setts the probability of not being caught during the study equal to the product of the probability of not being caught during each respective sampling period.

c.   Behavioral trap response – Model M_b

This model describes a change in capture probability after the first encounter with an animal. Typical notation is probability of capture for unmarked individuals - p_c and marked animals - p_r. This behavioral response can be positive (trap-happy), or negative (trap-shy). Thus, the model estimates only three parameters N, p_c, p_r.

The probability function for this model is:

$$P(x_w \mid N, p_c, p_r) = \frac{N!}{\left[\prod_{i=1}^{K} x_w!\right](N - M_{K+1})!} p_c^{M_{K+1}}$$
$$\times (1 - p_c)^{KN - M_{K+1} - M.}$$
$$\times p_r^{m.}(1 - p_r)^{M.-m.}$$

where

$$m. = \sum_{i=2}^{K} m_j ,$$

the number of recaptures during the study, and m_j is the number of marked animals caught on occasion j. Also, if M_j is the total number of marked animals in the population at j then

$$M. = \sum_{i=2}^{K} M_j ,$$

the total number of animals available for recapture, and M_{K+1} is the total number of animals marked in the study.

The probability of initial capture is the total number of first captures divided by the total number of first captures possible:

$$\hat{p}_c = \frac{M_{K+1}}{(KN - M)} ,$$

and the probability of recapture is

$$\hat{p}_r = m./M. ,$$

the number of recaptures divided by the number available for recapture. This model is equivalent to estimation under a removal (harvest) model.

d.   Heterogeneity among individuals – Model M_h

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This model is truly different conceptually from other models in that capture probabilities do not vary temporally or based on behavior, but each individual is assumed to have a unique capture probability. Conceptually, this model is parameterized as a random sample of capture probabilities ($p_1...p_N$) from some underlying distribution $F(p)$. Given a cell probability, π_j, which is basically the average probability that an individual is captured j times:

$$\pi_j = \int_0^1 \frac{K!}{(K-j)!\,j!} p^j (1-p)^{K-j} dF(p).$$

The model is described based on f_j, the number of animals caught on j occasions:

$$P(f_1...f_K \mid F) = \frac{N!}{\left[\prod_{i=1}^{K} f_i!\right](N - M_{K+1})!} \pi_0^{N - M_{K+1}} \prod_{i=1}^{K} \pi_i^{f_j} .$$

These models are not MLEs. Thus, it is not possible to use AIC or LRTs for model selection. Nonparametric MLEs for this model have been proposed by Norris and Pollock (1995, 1996). Pledger's (2000) mixture models are MLEs based on a finite number of groups with unique capture probabilities. The MLE models proposed by Huggins (1989, 1991) and Alho (1990) estimate capture probabilities using the familiar logit functions of individual covariates:

$$p_i = \frac{e^{X_i \beta_i}}{1 + e^{X_i \beta_i}} .$$

These approaches do not include N in the likelihood and estimates of abundance are based on the Horvitz and Thompson (1952) estimator, which is the sum of the inverse of the probability of capture at least once during the study across individuals:

$$\hat{N} = \sum_{i=1}^{M_{K+1}} \frac{1}{\hat{p}_i^*} ,$$

where

$$\hat{p}_i^* = 1 - \prod_{j=1}^{K} \left(1 - \hat{p}_i\right).$$

e. Combined models of capture probability

It is possible to cast models that include 2 or all 3 of the sources of variation described above. These models require additional constraints and assumptions, and Pledger (2000) used mixture models that are MLEs to describe the models M_{tb}, M_{bh}, M_{th}, and M_{tbh}.

7. Testing model assumptions
    a. Closure

All 8 of the above models assume no change in N during the study. Two general approaches have been proposed for testing

1) The null hypothesis test in program CAPTURE (Otis et al. 1978) compares the p_{ij} (probability of capture for individual i at time j) for all individuals captured

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more than twice. The alternative hypothesis suggests that prior to first and subsequent to last capture some individuals had $p_{ij} = 0$, suggesting that they were recruited to the population sometime after the first or before the last capture period.

2) Pollock et al. (1974) suggested 4 hypothesis tests about time specific variation in the p_{ij}:

   a) No mortality and no recruitment.

   b) Mortality, but no recruitment

   c) Recruitment, but no mortality, and

   d) Recruitment and mortality.

Stanley and Burnham (1999) used this approach to test for overall population closure which basically compares a model of complete closure to a model for an open population. They present a series of contingency tables that decompose closure violations into the sources of violations (i.e., recruitment or losses), which correspond to the 4 tests described by Pollock et al. (1974 above).

b. Tag loss

Population estimates are biased high by tag loss. The exceptions are model M_b and M_{bh} since they do not rely on information on recaptures. Otherwise tag loss has been investigated with double-tagging studies.

8. Model selection

It is useful to choose models that balance the precision of estimates delivered by models with fewer parameters against the potential bias of more general models. Thus, we are seeking to select the simplest model that fits our data. However, many of the 8 models mentioned above are not based on likelihoods; it is not possible to base model selection on AIC (but see Pledger 2000). Otis et al. (1978) and Rexstad and Burnham (1991) describe an applicable approach based on goodness of fit and between-model tests.

a. Goodness of fit

The multinomial distributions can be used to calculate expected values that are compared to the observed values as we saw in the bootstrap GOF and RELEASE GOF for the CJS models. Program CAPTURE, which will run under MARK, computes these tests for 4 of the models – M_b, M_t, M_h, and M_{tb}. We will discuss goodness of fit along with open models in the next lecture.

b. Between model tests

Where MLEs can be computed for the models likelihood ratio tests can be used compare nested models (e.g., M_b and M_{tb}). These tests are conditional on the more general (i.e., parameterized) model fitting the data and ask whether the less general model adequately represents the data. CAPTURE compares models M_0 versus M_b and M_t and M_h and M_h versus M_{bh}.

c. Discriminant Analysis

Because AIC is not available for model selection, CAPTURE uses discriminant function analysis to compare models based on test statistics and probabilities.

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Stanley and Burnham (1998) describe a marginally improved approach that incorporates linear and multinomial discriminant functions. They also describe a method to incorporate model averaging.

Again the mixture models of Pledger (2000) are capable of emulating all 8 of the closed-populations models and several other variants in a likelihood framework that allows not only the use of AIC for model selection, but model averaging as well.

9.   Study design suggestions:

    a.   Minimize violation of model assumptions

        1)   Closure

            a)   Keep it short to maintain closure and minimize gains and losses.

            b)   Timing is everything – e.g., avoid periods of seasonal movements or dispersal

            c)   Trap mortality biases $\hat{N}$

            If substantial use removal models (behavioral response)

        2)   Use individual marks – methods really don't work with "batch marks."

    b.   Precision of estimates

        1)   High capture probabilities increase precision and reduce bias.

        2)   Increasing occasions ($\geq$ 5) increases precision

        3)   Parsimonious models increase precision

        4)   Behavioral response – problematic to "closure"

            a)   Pre-baiting – can minimize effects

            b)   Minimize trapping deaths – extreme behavioral response

            c)   Minimize handling time to reduce trap shyness

        5)   Heterogeneity

            a)   Stratify by important covariates (location, age, sex, etc.)

            b)   Covariates – use Huggins model

            c)   Distribution of trapping effort

                (1)   Trapping density v. home range

                (2)   Spatial arrangement

What we won't cover about closed models but you should know about

1.   Density Estimation with Capture-Recapture

    a.   Grids

    b.   Nested-grids

    c.   Trap webs

2.   Removal methods

3.   Change in ratio methods

Discussion

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1. Lincoln-Peterson two-sample method – basis for capture-recapture and capture removal models

2. *K*-sample method
    a. Complete set of models for all three sources of capture probability variation
    b. Some models not based on MLE
    c. Mixture models are promising solution

3. Density estimation
    a. Some methods estimate N first and then calculate density
    b. Gradient sampling methods are designed to estimate density

4. Considerations
    a. CMR - Best methods for difficult to observe animals
    b. Observational methods should be preferable for obvious reasons
    c. Removal methods useful for harvested populations

    General imprecise unless harvest is high relative to N