The simple Lincoln-Petersen estimator for population size is based on a single recapture occasion. If we generalize this design to allow for multiple recapture occasions we get substantially more flexibility to relax assumptions required by the L-P estimator. Multiple recaptures also enable us to get more precise estimates if assumptions of the L-P model are met.
Recall the assumptions of the L-P estimator:

1. All individuals are equally catchable;

2. Capture does not affect future capture probability;

3. Individuals do not lose marks.

For multiple captures we add the assumption:

1. Capture probability is constant through time.
If we simply extend the L-P model to one with multiple captures we change the structure of the data from binomial to multinomial.

Consider the simple L-P estimator.

- **Release**
  - **Captured**
  - **Not captured**

There are only 2 possibilities for marked animals: they are either captured or not captured.
With > 1 recapture occasion, however the number of capture histories increases as $2^n$, where $n$ is the number of recapture occasions.

With three recapture occasions there are 8 possible capture histories.
If $p$ is the probability of getting recaptured then we can write the probability of each capture history as follows:

$$P_{1111} = p \cdot p \cdot p \cdot p;$$

$$P_{1101} = p \cdot (1-p) \cdot p;$$

$$\cdots$$

$$P_{1001} = (1-p) \cdot (1-p) \cdot p,$$ etc.

Probability of getting the specific combination of capture histories from the previous slide is:

$$P = C \cdot (ppp)^{n_{1111}} \cdot (pp(1-p))^{n_{1110}} \cdot (p(1-p)p)^{n_{1101}} \cdot (p(1-p)(1-p))^{n_{1100}} \cdot$$

$$((1-p)pp)^{n_{1011}} \cdot (((1-p)p(1-p))^{n_{1010}} \cdot (((1-p)(1-p)p)^{n_{1001}} \cdot (((1-p)(1-p)(1-p))^{n_{1000}}$$
Now back to population estimation: for K recaptures and constant recapture probability (Model M₀) we only need to estimate two parameters: p and N (population size).

\[
P(\{x_\omega\} \mid N, p) = \frac{N!}{\prod_\omega x_\omega ! (N - M_{K+1})!} p^n (1 - p)^{KN - n}.
\]

Where \( n_\omega = \sum n_j \)

\( M_{K+1} = \text{number of unmarked animals caught} \)

\( X_\omega = \text{no. inds. With each capture history} \)

We use maximum likelihood to estimate N and p.
The expression for the probability of the data on the previous slide should look a lot like the expression we wrote for the probability of the data associated with the fate tree two slides back. \( C \) on the earlier slide is given by:

\[
\left[ \prod_\omega x_\omega ! \right] \frac{N!}{(N - M_{K+1})!}
\]

which is just the number of ways we could rearrange the individuals among capture histories.
\( n \) is the total number captured so \( p^n \) is the probability of capturing \( n \) individuals.

\( KN - n \) represents the number of individual capture opportunities for which a capture did not occur. Thus, 
\[(1 - p)^{(KN - n)}\] represents the probability of not capturing these individuals over the course of the study.
We can take the ln of the likelihood to turn it into a sum:

\[
\ln L(\{x_\omega\} \mid N, p) = \ln \left[ \prod_{\omega} \frac{N!}{x_\omega!(N - M_{K+1})!} \right] + (n. \ln(p)) + (KN - n.) \ln(1 - p)
\]

The estimator of \( p \) is given by:

\[
\frac{\partial}{\partial p} \ln L(p \mid N, \{x_\omega\}) = 0 \\
\Rightarrow \\
n. \hat{p}(N) = \frac{KN - n.}{1 - \hat{p}(N)} \\
\Rightarrow \\
\hat{p}(N) = \frac{n.}{KN}
\]
For a given data set, an estimate of $N_0$ is found by trial and error (there is a little more to it than this [Otis et al. 1978]), which is used in the formula on the previous slide to estimate $p$.

\[
\hat{p} = \frac{n}{K\hat{N}_0}
\]

We plug the formula for $\hat{p}$ into the likelihood and maximize with respect to $N$ to produce an estimate for $N$. This looks like:

$$
\ln L(\{x_\omega\} \mid N, p) = \ln \left[ \frac{N!}{\prod_\omega x_\omega! (N - M_{K+1})!} \right] + (n_\omega) \ln \left( \frac{n_\omega}{KN} \right) + (KN - n_\omega) \ln \left( 1 - \frac{n_\omega}{KN} \right)
$$
The ML estimator of \( N \) satisfies:

\[
\ln L(\hat{N}_0, \hat{p}(\hat{N}_0) | X) = \max \left[ \ln L(\hat{p}(N) | X, N) \right]
\]

\[
= \max \left[ \ln \left( \frac{N!}{(N - M_{K+1})!} \right) + (n.)\ln(n.) + (KN - n.)\ln(KN - n.) - KN\ln(KN) \right]
\]
For only two capture occasions there is a closed form (non-numeric) solution:

\[
\hat{N} = \frac{(n_1 + n_2)^2}{4m_2}
\]

\(n_i\) = number of captures on each occasion
\(m_2\) = number of recaptures on the second occasion
For the model in which we allow capture probabilities to vary among capture occasions (Model $M_t$) we need to estimate a larger number of parameters.

The probability distribution for the data under model $M_t$ is:

$$P\left(\{x_\omega\} \mid N, p\right) = \frac{N!}{\prod_\omega x_\omega! (N - M_{K+1})!} \times \prod_{j=1}^{K} p_j^{n_j} (1 - p_j)^{N-n_j}$$

Note that in this model there is a unique $p_j$ for each capture occasion.
The model has $K + 1$ parameters, $N$ and $\rho_1, \ldots, \rho_K$.

$N$ and the $\hat{\rho}_j$ are estimated by maximum likelihood.

\[ \hat{p}_j = \frac{n_j}{N} \]
Individual heterogeneity in capture probability adds complexity to the models we have considered. So far, we have considered models in which there were a limited number of parameters. If individuals vary in their capture probabilities, then potentially every individual could have a unique capture probability.
The mathematics of addressing this problem can be daunting, and involve approaches to reducing the number of parameters that need to be estimated.

Pledger (2000) has developed finite mixture models (building on earlier work by others). These models allow for a limited number of groups, each of which has its own capture probability.

For example if we assume two groups (with high and low capture prob.) we can write capture probability as:

\[ p = \pi p_L + (1 - \pi) p_H \]
We can now substitute this expression into the likelihood for model $M_0$ to estimate parameters: $N, \pi, p_L, p_H$.

Pledger’s method allows for more than two groups and could be applied to time varying or behavioral models.