# BIOL 410 Population and Community Ecology 

Mark Recapture
Calculating vital rates

## Mark Recapture methods

1. Capture and mark individuals

- Radio transmitters, PIT tags, ear tags, physical features, genetics, etc.

2. Recapture or resight random sample of individuals during subsequent surveys
3. Calculate the proportion of new and previously captured/ sighted individuals.

## Mark-Recapture Methods

Three Standard Methods

1. Petersen Method - closed population, single recapture event
2. Schnabel Method - closed population, multiple recapture events
3. Jolly-Seber Method - open population, multiple censusing events

- Closed population: doesn't change in size during study
- Open population: population changes in size


## Petersen Method

One mark and one recapture session

$M=$ Number of individuals marked during the first sample
$C=$ Total number of individuals captured during the second sample
$R=$ Number of individuals in the second sample that were marked
$N=$ Size of the population at the time of Marking.

## Petersen Method

- If the number of recaptures is less than $7(R<7)$, add the value of 1 to each of the number Marked, Captured and Recaptured

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

## Petersen - Confidence Intervals

How you Calculate Confidence Intervals depends on number of Recaptures relative to Total Captures at second marking session.

- If the proportion of recaptured individuals is greater than $10 \%$ of the total captures on the second sampling period ( $R / C>0.1$ ), then use a Binomial Confidence Interval.
- If $R / C$ is less than $10 \%$, but the number of recaptures is greater than 50 ( $\mathrm{R}>50$ ), then use a Normal Approximation
- If $R / C$ is less than $10 \%$ and $R<50$, you use a Poisson Confidence Interval


## Petersen - Confidence Intervals

## Binomial Confidence Interval

- X-axis = Recaptures /Captures
- Lines -Captures
- Y-Axis - Upper and lower Confidence Intervals for a given $\mathrm{R} / \mathrm{C}$.

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

Lower $95 \%$ CI on $\widehat{N}=\frac{1}{\text { Upper pop.proportion }} M$ Upper $95 \%$ CI on $\widehat{N}=\frac{1}{\text { Lower pop.proportion }} M$


## Petersen - Confidence Intervals

## Poisson Confidence Interval

- X in table corresponds to number of
Recaptures in your sample (R)
- Sub upper and lower values into estimate of $\mathbf{N}$ for low recaptures to get upper and lower Cl

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

TABLE 2.1 CONFIDENCE LIMITS FOR A POISSON FREQUENCY DISTRIBUTION. Given the number of organisms observed ( $x$ ), this table provides the upper and lower limits from the Poisson distribution. Do not use this table unless you are sure the observed counts are adequately described by a Poisson distribution.

| $x$ | 95\% |  | 99\% |  | $x$ | 95\% |  | 99\% |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | . Lower | Upper | Lower | Upper |  | Lower | Upper | Lower | Upper |
| 0 | 0 | 3.285 | 0 | 4.771 | 46 | 34.05 | 60.24 | 29.90 | 65.96 |
| 1 | 0.051 | 5.323 | 0.010 | 6.914 | 47 | 34.66 | 61.90 | 31.84 | 66.81 |
| 2 | 0.355 | 6.686 | 0.149 | 8.727 | 48 | 34.66 | 62.81 | 31.84 | 67.92 |
| 3 | 0.818 | 8.102 | 0.436 | 10.473 | 49 | 36.03 | 63.49 | 32.55 | 69.83 |
| 4 | 1.366 | 9.598 | 0.823 | 12.347 | 50 | 37.67 | 64.95 | 34.18 | 70.05 |
| 5 | 1.970 | 11.177 | 1.279 | 13.793 | 51 | 37.67 | 66.76 | 34.18 | 71.56 |
| 6 | 2.613 | 12.817 | 1.785 | 15.277 | 52 | 38.16 | 66.76 | 35.20 | 73.20 |
| 7 | 3.285 | 13.765 | 2.330 | 16.801 | 53 | 39.76 | 68.10 | 36.54 | 73.62 |
| 8 | 3.285 | 14.921 | 2.906 | 18.362 | 54 | 40.94 | 69.62 | 36.54 | 75.16 |
| 9 | 4.460 | 16.768 | 3.507 | 19.462 | 55 | 40.94 | 71.09 | 37.82 | 76.61 |
| 10 | 5.323 | 17.633 | 4.130 | 20.676 | 56 | 41.75 | 71.28 | 38.94 | 77.15 |
| 11 | 5.323 | 19.050 | 4.771 | 22.042 | 57 | 43.45 | 72.66 | 38.94 | 78.71 |
| 12 | 6.686 | 20.335 | 4.771 | 23.765 | 58 | 44.26 | 74.22 | 40.37 | 80.06 |
| 13 | 6.686 | 21.364 | 5.829 | 24.925 | 59 | 44.26 | 75.49 | 41.39 | 80.65 |
| 14 | 8.102 | 22.945 | 6.668 | 25.992 | 60 | 45.28 | 75.78 | 41.39 | 82.21 |
| 15 | 8.102 | 23.762 | 6.914 | 27.718 | 61 | 47.02 | 77.16 | 42.85 | 83.56 |
| 16 | 9.598 | 25.400 | 7.756 | 28.852 | 62 | 47.69 | 78.73 | 43.91 | 84.12 |
| 17 | 9.598 | 26.306 | 8.727 | 29.900 | 63 | 47.69 | 79.98 | 43.91 | 85.65 |
| 18 | 11.177 | 27.735 | 8.727 | 31.839 | 64 | 48.74 | 80.25 | 45.26 | 87.12 |
| 19 | 11.177 | 28.966 | 10.009 | 32.547 | 65 | 50.42 | 81.61 | 46.50 | 87.55 |
| 20 | 12.817 | 30.017 | 10.473 | 34.183 | 66 | 51.29 | 83.14 | 46.50 | 89.05 |
| 21 | 12.817 | 31.675 | 11.242 | 35.204 | 67 | 51.29 | 84.57 | 47.62 | 90.72 |
| 22 | 13.765 | 32.277 | 12.347 | 36.544 | 68 | 52.15 | 84.67 | 49.13 | 90.96 |
| 23 | 14.921 | 34.048 | 12.347 | 37.819 | 69 | 53.72 | 86.01 | 49.13 | 92.42 |
| 24 | 14.921 | 34.665 | 13.793 | 38.939 | 70 | 54.99 | 87.48 | 49.96 | 94.34 |
| 25 | 16.768 | 36.030 | 13.793 | 40.373 | 71 | 54.99 | 89.23 | 51.78 | 94.35 |
| 26 | 16.77 | 37.67 | 15.28 | 41.39 | 72 | 55.51 | 89.23 | 51.78 | 95.76 |

## Petersen - Assumptions

## Assumptions of the Petersen Method

- The Population is closed, so that N is constant
- All animals have the same chance of getting caught in the first sample
- Marking individuals does not affect their catchability
- Animals do not lose marks between the two sampling periods
- All marks are reported upon discovery in the second sample



## Schnabel Method

## Extension of Petersen Method with multiple marking events

- Number of Marked individuals accumulate with each time interval.

$$
\widehat{N}=\frac{\sum_{t}\left(C_{t} M_{t}\right)}{\sum_{t} R_{t}}
$$

- $C_{t}=$ Total number of individuals caught in sample $t$
- $R_{t}=$ Number of individuals already marked when caught at sample $t$
- $U_{t}=$ Number of individuals marked for first time and released in sample $t$
- $M_{t}=$ The number of marked individuals in the population just before sample $t$ is taken. (essentially, the cumulative number of $U_{t}$ up to $t-1$ )

$$
-\quad \mathrm{M} 6=\mathrm{U} 1+\mathrm{U} 2+\mathrm{U} 3+\mathrm{U} 4+\mathrm{U} 5+\mathrm{U} 6
$$

## Schnabel - Confidence Intervals

If $\sum R_{t}<50$, use values from a Poisson table

If $\sum \boldsymbol{R}_{\boldsymbol{t}}>5$, calculate with a normal approximation

$$
\frac{1}{\hat{N}} \pm t_{\alpha} \text { S.E. }
$$

where S.E. $=$ standard error of $1 / \mathrm{N}$
$t_{\alpha}=$ value from Student's t-table for $(100-\alpha) \%$ confidence limits.

## Schnabel - Confidence Intervals

If $\sum R_{t}>50$, calculate with a normal approximation

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\frac{1}{\hat{N}} \pm t_{\alpha} \mathrm{S} . \mathrm{E} .
$$

where S.E. $=$ standard error of $1 / \mathrm{N}$
$t_{\alpha}=$ value from Student's t-table for (100- $\alpha$ ) \% confidence limits.

$$
\begin{gathered}
\text { Variance }\left(\frac{1}{\hat{N}}\right)=\frac{\sum R_{t}}{\left(\sum C_{t} M_{t}\right)^{2}} \\
\text { Standard error of }\left(\frac{1}{\hat{N}}\right)=\sqrt{\operatorname{Variance}\left(\frac{1}{\hat{N}}\right)}
\end{gathered}
$$

## Vital rates

- Fundamental parameter of population change: birth rates, death rates
- Birth rates: number of individuals born/individual
- Death rates: number of individuals die/individual
- Probability of survival $=1-\mathrm{P}$ (mortality)
- Why are population ecologists interested in vital rates?


## Birth rates: Fecundity

- "number of female offspring produced per adult female per unit of time"
- Often generalized to the number of young produced per female per unit of time
- If interested in population productivity then must know the sex ratio of the young
- "Young" often constituted as:
- Number of zygotes
- Number of viable young
- Number of individuals recruited into next time step
- Natality is synonymous with birth rate
- Ratio of live births in area to population of area (births/1000 individuals/year)


## Measuring birth rates

- Direct methods
- Observe number of offspring at natal site
- Some mammal and birds (eggs, litter size)
- Link between adult and offspring (somewhat)
- Observe number of young at breeding site
- Weak or no link between adult and offspring
- Placental scars from managed mammal populations


## Measuring birth rates

- Indirect methods
- Evidence of offspring at different stages



Upstream spawning trap


Female weight Gonadal weight


Egg weight GSI estimate


Estimate fry per redd

## Measuring mortality rates

- Finite Survival
- Alive or dead (finite)
- $P($ mortality $)=1-P($ survival $)$
- \# of individuals alive at end of a time period / \# of individuals alive at beginning of a time period
- Finite survival rate (e.g. year)

$$
\hat{S}_{0}=\frac{N_{1}}{N_{0}}=\frac{80}{100}=80 \%
$$

- Year is a convenient period, but could be any duration (e.g. month, 17 days, etc.)


## Measuring mortality rates

- Finite survival rate
- Converting from observed rate to mortality over standard time
- E.g. 54 of 67 individuals alive over 42 day period (cohort frogs)

$$
\text { Adjusted } \hat{S}_{0}=\text { Observed } \widehat{S}_{0}{ }^{\left(t_{s} / t_{0}\right)}
$$

- $\mathrm{t}_{\mathrm{s}}=$ standardized time interval (e.g. 30 days)
- $t_{0}=$ observed time interval (e.g. 42 days)
- Standardize to 30 day period

Observed $\widehat{S}_{0}{ }^{\left(t_{s} / t_{0}\right)}=$ Observed $\widehat{S}_{0}{ }^{\left(t_{s} / t_{0}\right)}=(54 / 67)^{(30 / 42)}=0.8^{0.71}=0.86$

## Measuring mortality rates

- Instantaneous survival rate
- If number of deaths over a very short time is proportional to the number of individuals


Instantaneous mortality rate Always a negative number

Integral form

$$
N_{t}=N_{0} e^{i t}
$$

## Finite survival rate



$$
\begin{aligned}
& \hat{S}_{0}=\frac{50}{100}=50 \% \\
& \hat{S}_{0}=\frac{75}{100}=70 \%
\end{aligned}
$$

Time

## Survival rates



## Survivorship curves



## Measuring survival/mortality rates

- For some species survival is the dominant determinant of populations change
- Survival can be a difficult process to quantify in wild populations
- Survival of captive animals is usually a poor indicator of survival of wild animals


## Methods for estimating survival rates

1. Life history table

- Age-specific description of a mortality schedule
- Cohort life history table superior to static life table

| $\boldsymbol{x}$ | $\boldsymbol{S}(\boldsymbol{x})$ | $\boldsymbol{l}(\boldsymbol{x})$ | $\boldsymbol{g}(\boldsymbol{x})$ | $\boldsymbol{b}(\boldsymbol{x})$ | $\boldsymbol{l}(\boldsymbol{x}) \boldsymbol{b}(\boldsymbol{x})$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 0 | 500 | 1.0 | 0.8 | 0 | 0.0 |
| 1 | 400 | 0.8 | 0.5 | 2 | 1.6 |
| 2 | 200 | 0.4 | 0.25 | 3 | 1.2 |
| 3 | 50 | 0.1 | 0 | 1 | 0.1 |
| 4 | 0 | 0 |  | 0 | 0.0 |

## Methods for estimating survival rates

1. Life history table
2. Known fate approaches

- Mark and relocate individuals
- Collars on animals, relocate plants
- Relocate individuals regularly/semi regularly
- Record time to mortality or proportion of individuals alive



## Methods for estimating survival rates

2. Known fate approaches

- Average daily survival
- Mayfield's estimator for daily nest survival:

$$
\hat{S}=1-\frac{\# \text { deaths }}{\text { Exposure days }}
$$

Deaths per exposure day

$$
\hat{S}=1-\frac{\# \text { deaths }}{\text { Exposure days }- \text { number censored animals }}
$$

## Methods for estimating survival rates

2. Known fate approaches

- Average daily survival (Trent and Rongstad 1974)

$$
\hat{S}=\frac{x-y}{x}
$$

$\hat{S}=$ estimate of the finite daily survival rate $x=$ total number of animal days observed over the period
(number of animals * observation days)
$y=$ total number of deaths observed over the period

## Methods for estimating survival rates

2. Known fate approaches

- Average daily survival

| Interval between <br> relocation (day) | \# animals relocated | \# Survivors | \# Deaths |
| :--- | :--- | :--- | :--- |
| 1 | 47 | 45 | 2 |
| 2 | 23 | 22 | 1 |
| 3 | 36 | 33 | 3 |
| 4 | 12 | 12 | 0 |
|  |  |  |  |
| $=\frac{x-y}{x}$ | $0.9759=$ | $(47)(1)+(23)(2)+(36)(3)+(12)(4)-6$ |  |

## Methods for estimating survival rates

2. Known fate approaches

- Convert daily rates to other time interval:

$$
\hat{p}=\hat{S}^{n} \quad \text { or } \quad \text { Adjusted } \hat{S}_{0}=\text { Observed } \widehat{S}_{0}^{\left(t_{s} / t_{0}\right)}
$$

$p=$ estimate of finite survival rate per $n$ days
$\hat{S}=$ estimated finite daily survival rate
$\mathrm{n}=$ number of days to upscale estimate

$$
0.4810=0.9759^{30}
$$

# Methods for estimating survival rates Survival analysis 

- Examines and models the time it take for events to occur
- The event can be death, therefor "Survival analysis"
- Other names
- "event-history analysis" : sociology
- "failure-time analysis" : engineering
- Advantages:
- Marked individuals checked on non-regular schedules
- New left-censored individuals added to samples so that large n retained: "staggered entry design"
- Accounts for right censored data - individuals lost to monitoring, but not assumed to have died
- Right censored: unknown fate, radio failure or loss, emigration from study area.


## Censoring: dealing with uncertain data

- Censored survival times:
- problem when event has not occurred (within the observation time) or the exact time of event is not known.
- Right censoring:
- Where the date of death is unknown but is after some known date
- true survival time > observed survival time
e.g.
- Organism alive at end of the observation period (study)
- Subject is removed from the study
- animal escapes, animal gets lost, plant gets eaten, etc.


## Censoring

- Left censoring:
- Occurs when a subject's survival time is incomplete on the left side of the follow-up period.
- True survival time < Observed survival time
- Exact timing of event is uncertain: e.g..
e.g.
- We want to know time to death, but only assess survival when sampling

Censoring must be independent of the event being looked at

## Censoring



## Estimated/Empirical survival curves

- Survival curve is estimated by Kaplan-Meier (KM) estimator, also know as "product estimator"
- The Kaplan-Meier estimate is a nonparametric maximum likelihood estimate of the survival function, $\mathrm{S}(\mathrm{t})$
- The estimate is a step function with jumps at observe event times


## Kaplan-Meier estimate



## Kaplan-Meier estimate

$$
\hat{S}_{K M}=\prod_{t_{i}<t}\left[1-\left(\frac{d\left(t_{i}\right)}{r\left(t_{i}\right)}\right)\right]
$$

| Sample <br> period | \# birds <br> with radios | \# found <br> dead | \# censored | \# added | Survival <br> estimate |
| :--- | :--- | :--- | :--- | :--- | :--- |
| 1 | 20 | 0 | 0 | 1 | 1 |
| 2 | 21 | 0 | 0 | 1 | 1 |
| 3 | 22 | 2 | 1 | 0 | 0.909 |
| 4 | 19 | 5 | 0 | 0 | 0.670 |

$$
0.67=\prod_{t_{i}<t}\left[\left(1-\left(\frac{0}{20}\right)\right)\left(1-\left(\frac{0}{21}\right)\right)\left(1-\left(\frac{2}{22}\right)\right)\left(1-\left(\frac{5}{19}\right)\right)\right]
$$

