

Stat 534: formulae referenced in lecture, week 5, part 2:  
 Overparameterized models and models accounting for individual heterogeneity  
 Corrected, 30 Sept 21

Mtb: both behavioural response and time-dependent capture probabilities

- Our first encounter with an overparameterized mark-recapture model
- For 3 occasions: 6 parameters, 3  $p$ 's, 2  $c$ 's (no  $c_1$ ) and 1 N
- Let's work out the capture probabilities

Time			# animals	probability
1	2	3		
Y	Y	Y	$n_{111}$	$p_1 c_2 c_3$
Y	Y	N	$n_{110}$	$p_1 c_2 (1 - c_3)$
Y	N	Y	$n_{101}$	$p_1 (1 - c_2) c_3$
Y	N	N	$n_{100}$	$p_1 (1 - c_2) (1 - c_3)$
N	Y	Y	$n_{011}$	$(1 - p_1) p_2 c_3$
N	Y	N	$n_{010}$	$(1 - p_1) p_2 (1 - c_3)$
N	N	Y	$n_{001}$	$(1 - p_1) (1 - p_2) p_3$
N	N	N	$n_{000}$	$(1 - p_1) (1 - p_2) (1 - p_3)$

- Nothing looks amiss here, so let's count sufficient statistics
- based on the patterns for Mt and Mb, you would expect:
  - $n_i$ : number caught at time  $i$
  - $m_i$ : number marked caught at time  $i$
  - $M_{t+1}$ : total number of unique individuals seen
- Looks like 6 sufficient statistics, enough to estimate 6 parameters
- But:  $M_{t+1}$  is not “new” information. It can be computed from  $n_i$  and  $m_i$ 
  - # 1st seen at time 1 + # first seen at time 2 + # first seen at time 3
  - =  $n_1 + (n_2 - m_2) + (n_3 - m_3)$
- so no unique solution! Many sets of parameters have the same lnL
- Sometimes can spot redundancy by examining the capture history probabilities
- Have a problem when two parameters only appear multiplied or added together, e.g.  $\theta_1 \theta_2$  or  $\theta_1 + \theta_2$
- Numerical assessments:

- look at the rank of the negative Hessian matrix (= # non-zero eigenvalues)
- often, use very small (e.g.,  $< 0.005$ ) because of numerical issues computing the Hessian
- For one particular data set, the eigenvalues were:  
44.1339 25.0000 20.8004 18.6077 0.0022 0.0015  
Two parameters have very large variances, so can not be identified
- or look for massive standard errors for one or more parameters

Solutions for overparameterized models:

- Simplify the model, e.g. reparameterize  $\theta_1\theta_2$  as a single parameter
- Put constraints on the parameters
- E.g., for Mtb you could:
  - Make time effects follow a logistic regression

$$\text{logit } p_i = \log \left( \frac{p_i}{1 - p_i} \right) = \beta_0 + \beta_1 i$$

- Connect recapture and capture probabilities, also usually by a logistic

$$\text{logit } c_i = \nu + \text{logit } p_i$$

Model Mh: allows each of the  $N$  individuals to have a different  $p_i$

- The capture history for five **individuals**:

Time			# animals	probability
1	2	3		
Y	Y	Y	1	$p_1^3$
Y	Y	Y	1	$p_2^3$
Y	Y	N	1	$p_3^2(1 - p_3)$
N	N	N	1	$(1 - p_4)^3$
N	N	N	1	$(1 - p_5)^3$

- Sufficient statistics are the # captures and # missed for each of the  $M_{t+1}$  animals seen at least once
- There are  $M_{t+1}$  sufficient statistics, but  $N+1$  parameters
- Can't estimate  $N$  without modeling  $p_i$  or using a completely different approach (coverage)

Modeling  $p_i$  using a Beta( $a,b$ ) distribution

- $f(p|a,b) = \frac{\Gamma(a+b)}{\Gamma(a)\Gamma(b)} p^{a-1} (1-p)^{b-1}$ 
  - $\Gamma(x)$  is the gamma function
  - Uniform(0,1) is Beta(1,1)
  - Hand drawn pictures
  - Key is that all are unimodal except when peaks are at 0 or 1
- mean:  $\mu_p = E p = \frac{a}{a+b}$
- variance:  $\text{Var } p = \frac{ab}{(a+b)^2(a+b+1)} = \mu_p(1-\mu_p)\frac{1}{a+b+1}$
- The approach:
  - Estimate  $a$  and  $b$  from the capture histories of the  $M_{t+1}$  observed individuals
  - Assume all  $N$  individuals have capture probabilities from that Beta( $a, b$ ) distribution
  - Provides sufficient information to estimate  $N$
- Ken Burnham worked on this model extensively in the 1980's
- Great idea in theory, didn't work in practice
- Problem is that capture probabilities are more complicated than can be modeled by a Beta distribution

Pledger heterogeneity models (2000)

- For now, focus on Mh: no time or behavioural effects
- $p_i$  = probability individual  $i$  is captured on an occasion
- $P[\text{capture history} | p_i] = P[\text{capture history} | p_i] = \prod_{j=1}^t p_i^{X_{ij}} (1-p_i)^{(1-X_{ij})}$
- If don't know  $p_i$ , then want the marginal probability

$$P[\text{capture history}] = \int_{p_i=0}^1 f(\text{capture history} | p_i) f(p_i) d p_i$$

- Burnham's beta model used this idea with a beta distribution for  $f(p_i)$ 
  - beta and binomial distributions “play nicely” together
  - the integral has an analytical solution
- Shirley Pledger proposed a more flexible distribution for  $f(p_i)$

- finite mixture model:  $p_i$  has one of two values (could be 3 or more but 2 often sufficient)

$$f(p_i) = \begin{cases} \pi_1 & \text{with probability } f_1 \\ \pi_2 & \text{with probability } f_2 = 1 - f_1 \end{cases}$$

- So, the marginal distribution is a sum, not an integral, because  $p_i$  has only 2 values:

$$P[\text{capture history}] = \sum_{a=1}^2 f_a P[\text{capture history}|p_a]$$

- for 2 components: 3 parameters for capture probability:  $f_1, \pi_1, \pi_2$ .
  - More parameters if more than 2 mixture components,
  - e.g., for 3 components:  $f_1, f_2, \pi_1, \pi_2, \pi_3$

- Likelihood is (for 2 components):

$$L(N, f_a, \pi_1, \pi_2 | \{X_{ij}\}) = \frac{N!}{\text{constant} \times (N - M_{t+1})!} \prod_{i=1}^N \left[ \sum_{a=1}^2 f_a P[\text{capture history}|p_a] \right]$$

- lnL is not simple - includes log sum(stuff)
- Can generalize to include time and behavioural effects

Huggins model: relate  $p_i$  to one or more covariates,  $X_i$

- Logistic regression model:  $\text{logit}(p_i) = \log \frac{p_i}{1-p_i} = \beta_0 + \beta_1 X_i$

$$p_i = \frac{1}{1 + e^{-(\beta_0 + \beta_1 X_i)}}$$

- Not fit using the “usual” logistic regression algorithms
  - Only have data for individuals seen at least once - missing many of the 0’s
  - Need to model  $P[\text{capture history} | \text{captured at least once}]$

$$P[\text{capture history} | \text{captured at least once}] = \frac{P[(\text{capture history}) \& (\text{captured at least once})]}{P[\text{captured at least once}]}$$

- $P[\text{capture history and captured at least once}] =$  product of appropriate p or p and c terms (usual expression)
- Define  $p_{ij} = P[\text{capture individual } i \text{ on occasion } j]$
- $P[\text{captured at least once}] = 1 - P[\text{never captured}] = 1 - \prod_{j=1}^k (1 - p_{ij})$

- Huggins incorporated time and behavioural responses by adding
  - a unique value for each time
  - First captures: note time-specific intercept

$$\text{logit } p_{ij} = \beta_{0j} + \beta_1 X_i$$

- $c$  (recapture probs) have a fixed relationship to  $p$  (first capture probs)
- Recaptures: the  $p_{ij}$  model + a consistent trap-happy or trap-shy effect,  $\nu$

$$\text{logit } c_{ij} = \nu + \beta_{0j} + \beta_1 X_i = \nu + \text{logit } p_{ij}$$

- Provides a simple way to model  $c$  and  $p$
- What about estimating  $N$ ?
  - $N$  not in the likelihood
  - need some other way to estimate it

Huggins model: estimating  $N$

- Add up  $1/P[\text{seen at least once}]$  for each observed animal
- (Horvitz-Thompson estimator: Population Total  $Y = \sum_{i=1}^n Y_i/\pi_i$ )

$$\hat{N} = \sum_{i=1}^{M_{t+1}} \frac{1}{1 - \prod_{j=1}^t (1 - \hat{p}_{ij})}$$

- Can get a variance estimator (complicated, not illuminating)

Is Huggins  $\hat{N}$  a reasonable estimator?

- Prefer unbiased estimates.
  - $\hat{N}$  is a random variable.
  - Would like  $E \hat{N} = N$
  - i.e., sometimes  $\hat{N}$  is too high, sometimes too low, but on average spot on
- Is  $\hat{N}_{Huggins}$  unbiased?
  - Yes, if  $p_{ij}$  is known precisely
  - Define  $p_i(\theta) = P[\text{individual } i \text{ captured at least once} \mid \text{parameters } \theta]$
  - Define  $C_i = \begin{cases} 0 & \text{when individual not captured} \\ 1 & \text{when individual was captured} \end{cases}$

$$E \hat{N}_{Huggins} = E \sum_{i=1}^{M_{t+1}} \frac{1}{p_i(\theta)} = E \sum_{i=1}^N \frac{C_i}{p_i(\theta)} = \sum_{i=1}^N \frac{E C_i}{p_i(\theta)} = \sum_{i=1}^N \frac{p_i(\theta)}{p_i(\theta)} = N$$

- 3rd step requires known  $p_i(\theta)$
- In practice,  $p_i(\theta)$  is estimated, because coefficients in the models for  $p_{ij}$  and  $c_{ij}$  are estimated
- bias is small so long as sufficient data to provide good estimates of  $p_i(\theta)$

Sample Coverage (Chao heterogeneity estimators)

- Coverage: proportion of total capture probability associated with observed individuals

$$C = \frac{\sum_{i=1}^{M_{t+1}} p_i \mathbf{I}(\text{seen at least once})}{\sum_{i=1}^N p_i}$$

- Explanation / example in hand-written notes
- Notation:
  - $\bar{p}$  mean capture probability in the population
  - $\gamma$  c.v. of capture probabilities in the population
  - $n$  total # captures
  - $f_i$  # number of individuals seen  $i$  times, e.g.:
  - $f_1$  # number seen only once
  - $f_2$  # number seen twice, etc.
- Assume a particular model for the data (details in Chao & Lee 1992, 1994, not important)
  - use to derive expected values

$$\frac{\mathbf{E} M_{t+1}}{\mathbf{E} C} \cong N - \frac{n (1 - \bar{p})^{n-1}}{\mathbf{E} C} \gamma^2$$

- Need to estimate  $C$ ,  $\bar{p}$ , and  $\gamma$
- $\bar{p}$ :
  - Have  $p_i$  for observed individuals, but average is biased
  - More likely to observe individuals with large  $p_i$
  - $\bar{p}$  in the population can be estimated from  $f_1$ : # individuals seen only once

$$N \cong \frac{\mathbf{E} M_{t+1}}{\mathbf{E} C} + \frac{\mathbf{E} f_1}{\mathbf{E} C} \gamma^2$$

- $\gamma$ : sample cv not so obviously biased
- $C$ : an old estimator, from the 1950's

$$\hat{C} = 1 - \frac{f_1}{\sum_{i=1} t_i f_i}$$

– There is a bias corrected estimate, but really want unbiased estimates of  $1/\hat{C}$  and  $\gamma^2/\hat{C}$

- Putting the pieces together: applying the “plug-in” principle

$$\hat{N} = \frac{M_{t+1}}{\hat{C}} + \frac{f_1}{\hat{C}} \hat{\gamma}^2$$