WILD 502
The Robust Design: *combining closed and open populations*

Chapter 19 – *WNC book*
Chapter 15 – *C&W book* – chapter written by William Kendall

Quantities of interest in studies of population dynamics:

- State variable – population size
- Rate of change in state variable – population growth rate
- Vital rates responsible for change in state variable – births, deaths, and movement

To date in this course, we've considered models that estimate:

- Abundance (closed models)
- Population losses to mortality
    - True survival (known-fate models)
    - Apparent survival (CJS- and JS-models and their extensions)
- Movement among locations (multi-state models)
- Population gains (recruitment in J-S type models, e.g., POPAN)
- Rate of population change (lambda from J-S type models, e.g., Pradel)

Of course, we didn't get all we wanted from some of those quantities. For example,

- movement among locations was only relevant to the locations we actually sampled at.
- survival estimates were actually estimates of *apparent survival* for many of our models
- recruitment merged births *in situ* with immigrants from elsewhere

It would be nice to be able to do more with *immigration* and *emigration rates*, rates which can be very important to studies of spatially distributed populations that exchange individuals.

As we went through a number of the models above, we also learned about concerns about estimator robustness to assumption violations, especially assumptions about heterogeneity in capture probabilities, e.g., capture probability being the same for marked and unmarked individuals in J-S models.

Jolly-Seber model has:

- survival estimators that are quite robust to heterogeneity in capture probabilities
- abundance estimators that are *not* robust to heterogeneity in capture probabilities

Closed models exist that have:

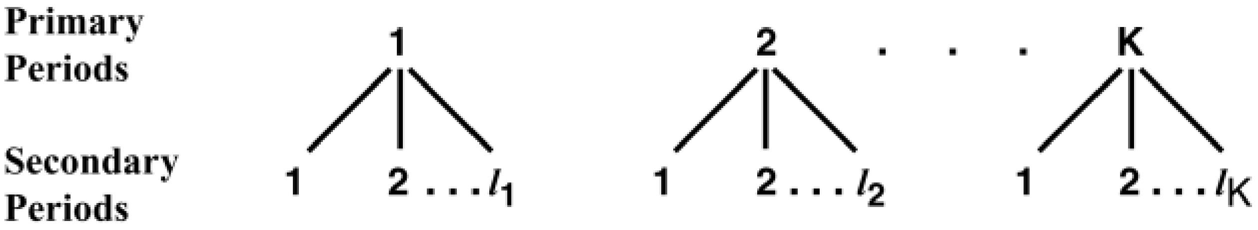
- abundance estimators that are robust to heterogeneity in capture probabilities

Pollock developed the Robust Design to take advantages of strengths of various approaches. The basic idea is to do so by sampling at two temporal scales:

- estimate abundance with closed models for data from short-term sampling
- estimate survival from open models using data from longer-term sampling
- estimate recruitment from the estimates produced for N_t and S_t.
- resulting estimators ought to be *robust* to various sources of heterogeneity in p

Pollock's (1982) Robust Design

- *K* primary sampling occasions spaced out such that expect mortality and recruitment between occasions, e.g., 1 year
- l_i secondary sampling occasions spaced at short intervals *within* each primary period, *i*



Example of design:

- K=4 or … 4 primary periods

- l_i = 3 for each primary period or … there are 3 secondary occasions for each of the 4 primary occasions

- Example EH for an animal - 110 001 011 000

- Refer to the EH as X_{gij} , which indicates if individual *g* was captured (1) or not (0) in secondary sampling period *j* of primary period *i*.

***Ad hoc* Approach to Robust Design**

1. Just use closed models and derive other parameter estimates – less common
2. Use combination of open and closed population-models – more common *ad hoc* approach
    a. Estimate N_i with closed models using data from secondary occasions of primary occasion *i*
    b. Estimate φ_i with open models (uses p_i^0)
    c. Estimate B_i with estimates from previous 2 steps - $\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i(\hat{N}_i - n_i + R_i)$

- **Steps are independent** = distinguishes *ad hoc* from method with single likelihood

- Use of 1 closed model for each of the K closed-model datasets is recommended to help ensure that magnitudes and directions of biases associated with estimates of N_i are consistent. This will lead to more reasonable estimates of recruitment.

- Can now obtain some parameters that CJS and/or JS wouldn't provide on their own:

- Even with full time-varying parameters, can now estimate:

    - $\hat{N}_1, \ldots, \hat{N}_K$
    - $\hat{p}_1, \ldots, \hat{p}_K$, which helps with confounding of other parameters
    - $\hat{\phi}_1, \ldots, \hat{\phi}_{K-1}$, e.g., can obtain last one as $\hat{\phi}_{K-1} = \dfrac{\phi_{K-1} p_K^*}{\hat{p}_K^*}$
    - $\hat{B}_1, \ldots, \hat{B}_{K-1}$

Two types of *p* in robust design

- p_{ij} – from secondary samples, refer to probability that an animal is captured on secondary occasion *j* of primary occasion *i* given that it is in the population on that occasion

    - model with closed models, which allow lots of flexibility for p_{ij}, in particular, individual heterogeneity
- p_i^* - from primary samples, refer to probability that an animal is *caught at least once* in primary occasion *i* (i.e., on at least one of the l_i secondary occasions) given that the animal is in the population during that sampling period

    - If assume no temporary emigration, can obtain from primary-occasion-only analysis

        - Can compare what you obtain from secondary occasions within a primary occasion to see if have evidence of temporary emigration (see below)

    - Survival estimates based on marked animals only

- Can now deal with permanent trap response at the level of the primary occasions, which was a problem in J-S model, although it does require extra work (see page 530 of *WNC*).

- If the same model is used for capture probability in all *K* closed models, there are 24 combinations of models that can be used for capture probabilities, where the models are M_α^β. where α specifies the model for the data from secondary occasions and β specifies the model for data from the primary occasions.

Table 1

Possible models that use complete capture history information under the robust design

Model	Source of variation in catchability	
	Within	Between
$M_{o}^{o(a)}$	None	None
$M_{o}^{t\,(a)}$	None	Time
$M_{t}^{o(a)}$	Time	None
$M_{t}^{t(a)}$	Time	Time
$M_{b}^{o(a)}$	Behavior	None
$M_{b}^{t\,(a)}$	Behavior	Time
$M_{b}^{b(a)}$	Behavior	Behavior
$M_{b}^{tb(a)}$	Behavior	Time, behavior
$M_{h}^{o(a,b)}$	Heterogeneity	None
$M_{h}^{t\,(a,b)}$	Heterogeneity	Time
$M_{tb}^{o\,(c)}$	Time, behavior	None
$M_{tb}^{t\,(c)}$	Time, behavior	Time
$M_{tb}^{b\,(b,c)}$	Time, behavior	Behavior
$M_{tb}^{tb(b,c)}$	Time, behavior	Time, behavior
$M_{th}^{o\,(a,b)}$	Time, heterogeneity	None
$M_{th}^{t\,(a,b)}$	Time, heterogeneity	Time
$M_{bh}^{o\,(a,b)}$	Behavior, heterogeneity	None
$M_{bh}^{t\,(a,b)}$	Behavior, heterogeneity	Time
$M_{bh}^{b\,(a,b)}$	Behavior, heterogeneity	Behavior
$M_{bh}^{tb\,(a,b)}$	Behavior, heterogeneity	Time, behavior
$M_{tbh}^{o\,(a,b)}$	All	None
$M_{tbh}^{t\,(a,b)}$	All	Time
$M_{tbh}^{b\,(a,b)}$	All	Behavior
$M_{tbh}^{tb\,(a,b)}$	All	Time, behavior

(a) Ad hoc approaches to estimation are available.

(b) Maximum likelihood estimators for population size cannot be computed without additional assumptions.

(c) Maximum likelihood estimation of all parameters is possible if a constant proportionality is assumed between capture and recapture probabilities.

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If there is no temporary emigration and all assumptions are met:

$$p_i^* = 1 - \prod_{j=1}^{l_i} (1 - p_{ij})$$

If there is temporary emigration, then that equation does not hold as we'll discuss below.

Assumptions:

For modeling secondary samples

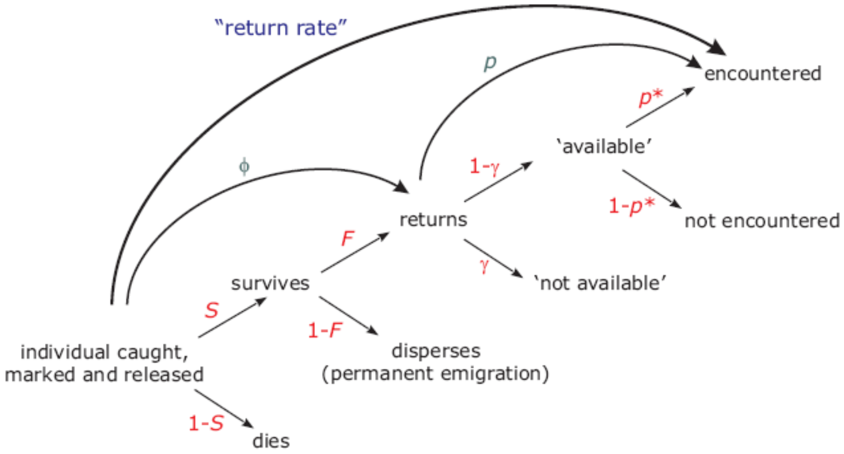
1. Population is closed to gains and losses during secondary periods within a primary occasion
2. Marks are neither lost nor incorrectly recorded
3. Capture probability over the secondary periods is modeled properly
4. Fate each animal with respect to capture probability is independent

For open modeling of data from primary periods

1. The conditional probability of surviving from period *i* to *i+1* is the same for all individuals
2. The conditional probability of being caught at each primary period is the same for each marked animal in the population at that time
3. Animal fates with respect to capture and survival are independent

Likelihood-Based Approach – a full likelihood is described for data from both primary and secondary periods. That likelihood includes the mathematical relationships among the capture parameters of the likelihood components for the two types of data. Because of that, temporary emigration must be considered. Temporary emigration, if ignored and of a certain form, results in biased estimates. Fortunately, likelihoods exist that handle temporary emigration as we'll see below. First, let's consider the underlying process that leads to the data we observe.

Decompose the probability of subsequent encounter – from Ch. 15 *CW*



Return rate = 'apparent survival rate' x 'apparent encounter probability'

$$R = \phi \times p$$

$$R = (SF) \times ([1-\gamma] p^*)$$

S: True survival rate

F: Fidelity or probability that don't permanently emigrate from study area

γ: Probability of temporary emigration from study area

p^*: Probability of detection given that the individual is present on the study area

Challenge:

Decompose φ and p into component pieces.

$$\phi = SF \quad \ldots \quad \hat{F} = \hat{\phi} / \hat{S}$$

$$p = (1-\gamma) p^* \quad \ldots \quad p^* = \hat{p}/(1\text{-}\hat{\gamma}) \quad \ldots \quad \hat{\gamma} = 1 - (\hat{p} / p^*)$$

Solution for γ:

- Estimate p from CJS modeling
- Estimate p^* from closed modeling = encounter probability for animals present
- Estimate γ from p and p^*

Structure of study design (see page 524 of *WNC* and the figure below from pages 15-4 of *CW*):

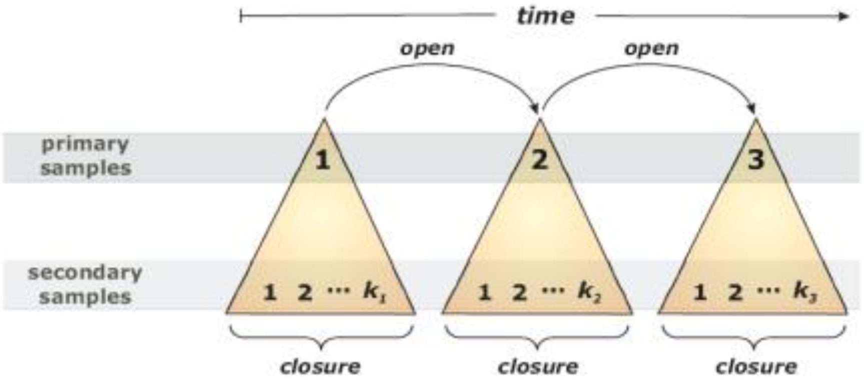


Figure 15.2: *Basic structure of 'classical' Pollock's robust design.*

Types of *p* used in readings

- p_{ij} – from secondary samples, refer to probability that an animal is capture on secondary occasion *j* of primary occasion *i*.
- p_i^* - or *p** from primary samples, refer to probability that an animal is caught at least once in primary occasion *i* given that the animal is in the population during that sampling period
  - $p_i^* = 1 - \prod_{j=1}^{l_i}(1 - p_{ij})$
- p_i^0 – (or *p* in Fig. 15.1 of *CW*) = probability of capture for all animals in the superpopulation at time *i* regardless of whether they are exposed to sampling efforts at *i* or not.
  - $p_i^0 = (1-\gamma)\left[1 - \prod_{j=1}^{l_i}(1 - p_{ij})\right]$
  - With no temporary emigration, γ=0 and $p_i^0 = p_i^*$

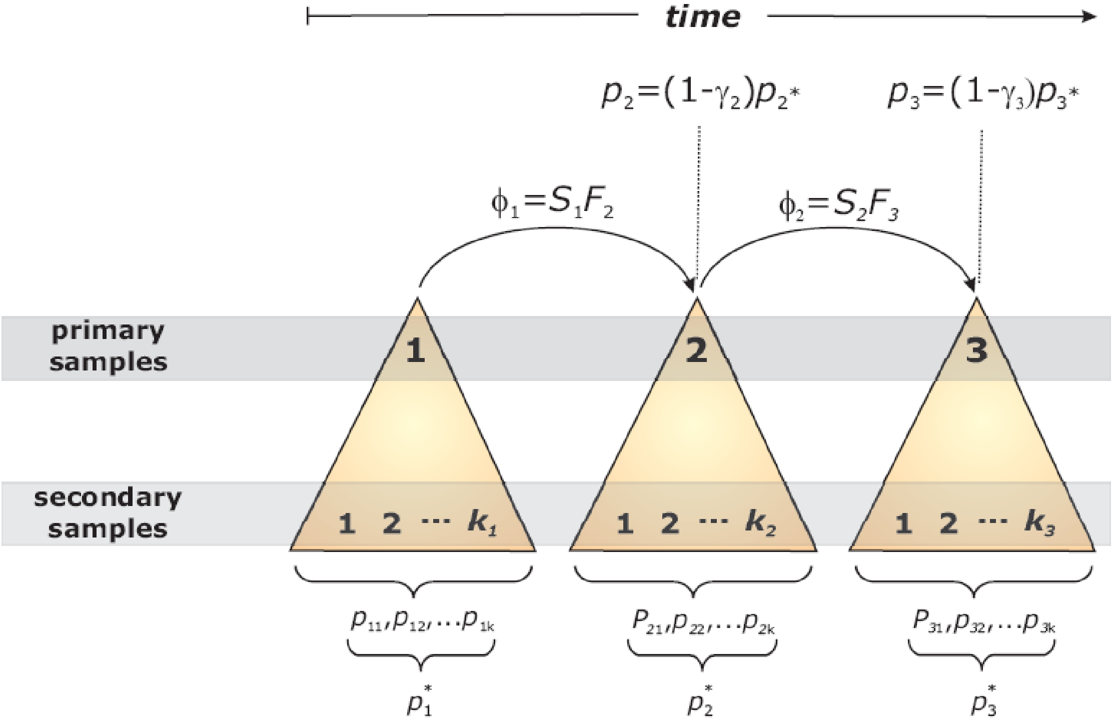


Figure 15.3: *Relationship of key parameters to basic structure of Pollock's robust design.*

Solution for *F* = use additional information:

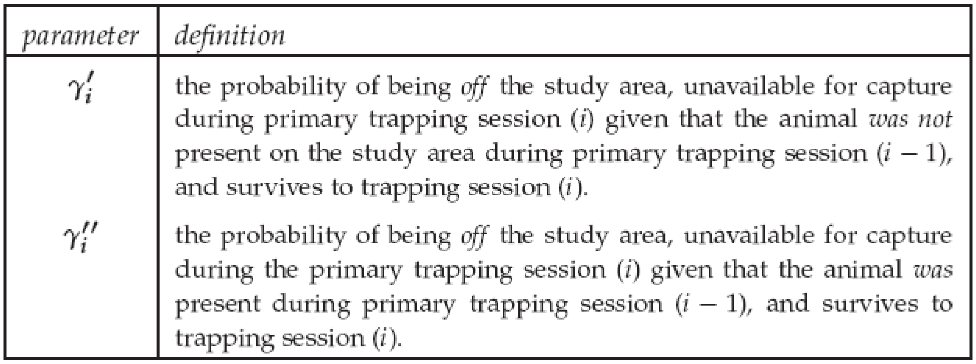
- For harvested population, recoveries of dead animals can be used to estimate *S*
- Incorporate telemetry data that allow known-fate modeling of *S*
- Other

Likelihood-Based Approach

Here, we use a full likelihood for data from primary and secondary occasions.
The likelihood is described in detail on page 536 of *WNC* and explained well there.

The full likelihood:

- is written products of components of the 2 types of data (closed & open)
- can include virtually any of the open models we've seen
- can include any of the closed models for which there's a likelihood that can be solved
- if temporary emigration occurs, careful consideration is needed
  - there are likelihood approaches and *ad hoc* approaches
  - consider whether temporary emigration has
    - a random pattern – *ad hoc* or likelihood approach works
    - a Markovian pattern – likelihood approach needed
    - no relevance, i.e., doesn't occur – *ad hoc* or likelihood works
    - likelihood allows model-selection to be readily done among competing models of movement process



parameter	*definition*
γ'_i	the probability of being *off* the study area, unavailable for capture during primary trapping session (i) given that the animal *was not* present on the study area during primary trapping session ($i-1$), and survives to trapping session (i).
γ''_i	the probability of being *off* the study area, unavailable for capture during the primary trapping session (i) given that the animal *was* present during primary trapping session ($i-1$), and survives to trapping session (i).

	Outside at time *t*	Inside at time *t*
Outside at *t+1*	$\gamma_i^{'}$	$\gamma_i^{''}$
Inside at *t+1*	$1-\gamma_i^{'}$	$1-\gamma_i^{''}$

- $\gamma_i^{''}$ = probability of **leaving** study area
- $1-\gamma_i^{''}$ = probability of **not leaving**

- $\gamma_i^{'}$ = probability of **staying away** given you've left
- $1-\gamma_i^{'}$ = probability of **returning** given you've left

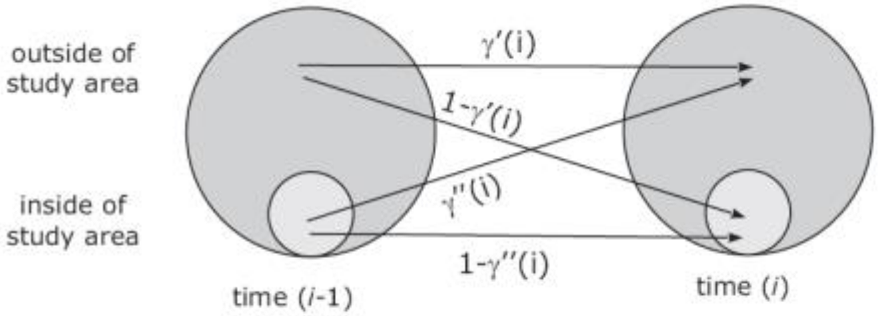


Figure 15.4: *Relationships between γ' and γ''. The larger circle represents the range of the super-population. The smaller circle (light grey) represents the part of the superpopulation that is available for encounter (i.e., in the study area), whereas the darker part of the larger circle represents individuals unavailable for encounter.*

View the EH for *K=3* & *l_i=3* for all *i* as: $1\ 1\ 1 \longrightarrow 1\ 1\ 1 \longrightarrow 1\ 1\ 1$

The probability that an animal is caught at least 1X in primary occasion *i* (with no Temp. Emigr.) is

$$p_i^* = 1 - [(1-p_{i1}) \times (1-p_{i2}) \times (1-p_{i3})]$$

Consider the following EH:

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Here's the probability associated with the *primary* intervals (we know it survived from *K=1 to K=3*)
The part in the brackets represents the different pathways that could lead to missing it on *K=2*

$$S_1S_2\left[\gamma''_2\left(1-\gamma'_3\right)+\left(1-\gamma''_2\right)\left(1-p^*_2\right)\left(1-\gamma''_3\right)\right]p^*_3$$

The following table shows the probability expressions corresponding to this encounter history

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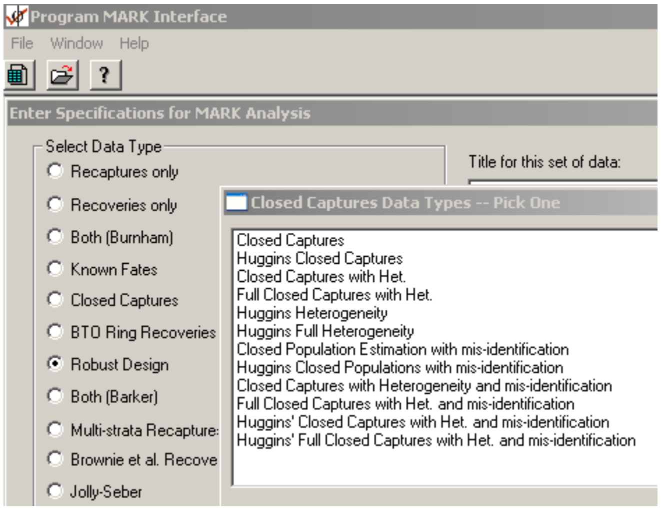
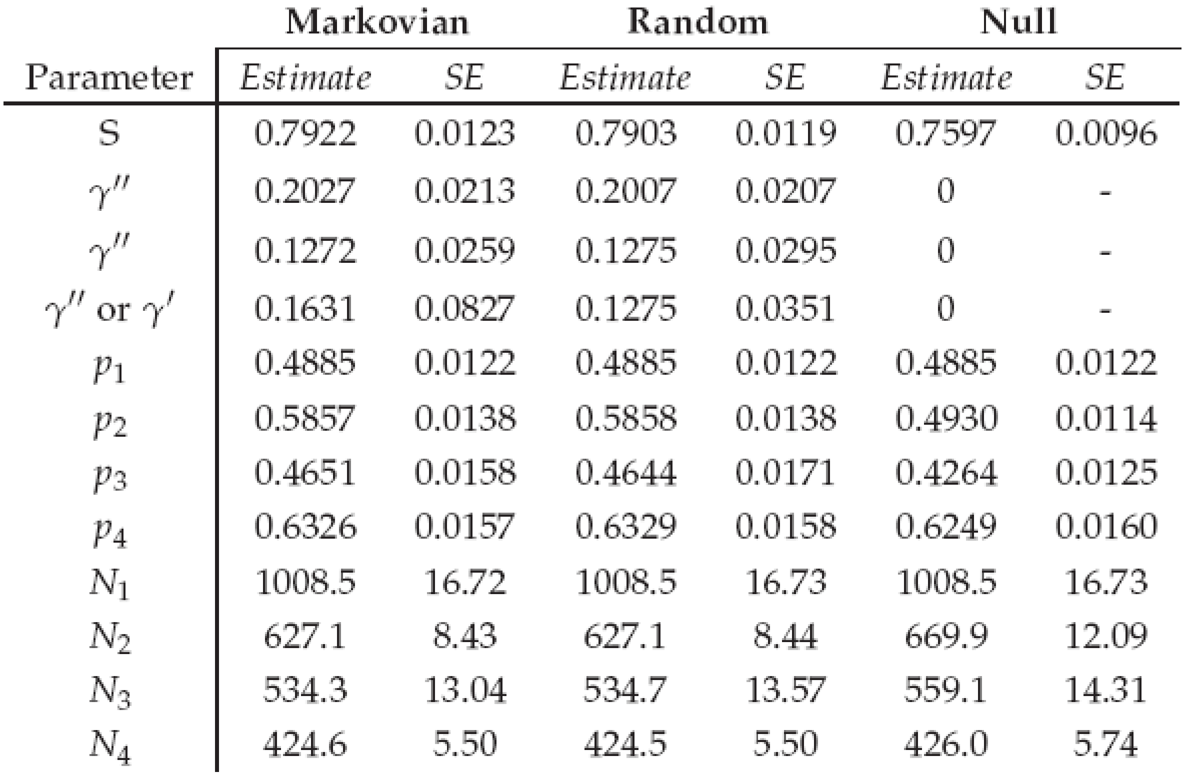
for both the Markovian and random temporary emigration models:

model	*probability*
Markovian	$\phi_1\gamma''_2\phi_2\left(1-\gamma'_3\right)p^*_3\phi_3\left(1-\gamma''_4\right)p^*_4$ $+\ \phi_1\left(1-\gamma''_2\right)\left(1-p^*_2\right)\phi_2\left(1-\gamma''_3\right)p^*_3\phi_3\left(1-\gamma''_4\right)p^*_4$
random	$\phi_1\gamma_2\phi_2\left(1-\gamma_3\right)p^*_3\phi_3\left(1-\gamma_4\right)p^*_4$ $+\ \phi_1\left(1-\gamma_2\right)\left(1-p^*_2\right)\phi_2\left(1-\gamma_3\right)p^*_3\phi_3\left(1-\gamma_4\right)p^*_4$



Select Data Type
- ○ Recaptures only
- ○ Recoveries only
- ○ Both (Burnham)
- ○ Known Fates
- ○ Closed Captures
- ○ BTO Ring Recoveries
- ● Robust Design
- ○ Both (Barker)
- ○ Multi-strata Recapture
- ○ Brownie et al. Recove
- ○ Jolly-Seber

Closed Captures
Huggins Closed Captures
Closed Captures with Het.
Full Closed Captures with Het.
Huggins Heterogeneity
Huggins Full Heterogeneity
Closed Population Estimation with mis-identification
Huggins Closed Populations with mis-identification
Closed Captures with Heterogeneity and mis-identification
Full Closed Captures with Het. and mis-identification
Huggins' Closed Captures with Het. and mis-identification
Huggins' Full Closed Captures with Het. and mis-identification



	Markovian		Random		Null	
Parameter	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*
S	0.7922	0.0123	0.7903	0.0119	0.7597	0.0096
γ''	0.2027	0.0213	0.2007	0.0207	0	-
γ''	0.1272	0.0259	0.1275	0.0295	0	-
γ'' or γ'	0.1631	0.0827	0.1275	0.0351	0	-
p_1	0.4885	0.0122	0.4885	0.0122	0.4885	0.0122
p_2	0.5857	0.0138	0.5858	0.0138	0.4930	0.0114
p_3	0.4651	0.0158	0.4644	0.0171	0.4264	0.0125
p_4	0.6326	0.0157	0.6329	0.0158	0.6249	0.0160
N_1	1008.5	16.72	1008.5	16.73	1008.5	16.73
N_2	627.1	8.43	627.1	8.44	669.9	12.09
N_3	534.3	13.04	534.7	13.57	559.1	14.31
N_4	424.6	5.50	424.5	5.50	426.0	5.74

The Robust Design combines in a single model the advantages of open- and close-models. Doing so provides advantages. Quoting loosely from chapter 15 of *CW* (page 15-11):

1. Estimates of p_i^*, and thus N_i and recruitment are less biased by heterogeneity in capture probability if you use heterogeneity models within season.

2. Temporary emigration can be estimated for several types of situations.

3. If temporary emigration does not occur, then abundance, survival, and recruitment can be estimated for all time periods. For example, in a 4-period study, half the parameters are inestimable using the JS method: all are estimable with the Robust Design method.

4. Precision tends to be better.

5. Multiple sessions within a season combined with closed-population models provide information on capture probability for the youngest catchable age class. Thus, estimation of recruitment into the second age class can be separated into (a) *in situ* recruitment and (b) immigration if there are only 2 identifiable age classes (3 are required if closed sessions aren't used).

6. The robust design's 2 levels of sampling allow for finer control over the relative precision of each parameter estimate.

In lab, we will see how the *ad hoc* approach and likelihood approach are implemented in MARK.

Extensions of Robust Design:

- Multiple ages
    - Recruitment components
    - If closed sampling allows estimation of p_{young}, then can separate
        - *in situ* reproduction
        - immigration from outside the study area
- Multiple groups
- Individual covariates
- Time-specific covariates
- Multistate
    - Movement among locations
    - Unobservable states, e.g., non-breeders that don't use study area
- Open robust design