Lecture 08 – Robust Design & Time symmetrical models

Pollock's Robust design

1. Readings

    Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563-578.

2. Resources

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

    Kendall, W. L. 1999. Robustness of closed capture-recapture methods to violations of the closure assumption. Ecology 80:2517-2525.

    Kendall, W. L., and J. D. Nichols. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. Journal of Applied Statistics 22:751-762.

    Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. Biometrics 51:293-308.

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

Time symmetrical models

1. Readings

    Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52:703-709.

2. Resources

    Pollock, K. H., D. L. Solomon, and D. S. Robson. 1974. Tests for mortality and recruitment in a k-sample tag-recapture experiment. Biometrics 30:77-87.

Robust Design

Changes in population size through time are a function of births, deaths, immigration, and emigration. The open population CMR models we have considered until now have only estimated apparent survival rates. That is, true survival, the portion of individuals surviving between sampling occasions is confounded with permanent emigration. I spoke briefly on closed models that assume that size of the population remained unchanged between sampling events. Robust design integrates the advantages of both types of models. Although this model is complicated, it brings more biological reality to the analysis of population dynamics. This method provides for the estimation of parameters that are not estimable under either open or closed models as well as more robust estimates of the familiar parameters of interest.

Although most CMR designs assume that captures occur instantaneously, this is rarely the case. Usually, data are aggregated from capture sessions that may last several days or weeks. The concept behind Pollock's Robust Design is to break these sessions into shorter sampling occasions, so that capture probabilities can be estimated among encounter occasions during these sessions. The primary assumption over CJS is that capture sessions are brief enough that we can assume population closure (i.e., no births, deaths, emigration, or immigration). Thus, closed models can be

used for the estimation of N or other parameters of interest, and integrated with open models to estimate true survival, temporary emigration, and immigration of marked animals back to the trapping area over the longer, open, "primary" sampling periods. Thus, the basic design is to sample over two temporal scales.

There is no disadvantage to using Robust Design other than the cost of sampling intensively enough to have more than one sampling occasion during each session.

Motivation

Early work by Robson (1969) and Pollock (1975) examined capture-history dependence in CJS estimators. But, CJS models could not be modified for heterogeneity or permanent trap response among individuals. While survival estimates from CJS are robust to this type of variation, open-model abundance estimators are not (Carothers 1973, 1979). Alternatively the CMR models for closed populations could incorporate these sources of variation.

Data Structure

The design consists of K **primary** sampling occasions separated by periods during which the population is assumed to be open. During each of the **primary** sampling occasions, the population is sampled at l **secondary** sampling occasions, during which the population is assumed to be closed. The number of secondary sampling occasions can vary among the primary sampling periods.

Robust design example, with 3 primary trapping sessions, each consisting of 4 secondary occasions.														
Primary periods K_i	1					2					3			
Secondary periods l_{ij}	1	2	3	4		1	2	3	4		1	2	3	4
Population status	Closed				Open	Closed				Open	Closed			

The resulting encounter history consists of the 12 live capture occasions with unequal time spacing. Secondary periods are specified in Program MARK as encounter occasions with time interval lengths of 0, and time intervals between primary periods have length >0.

Interval No.										
1	2	3	4	5	6	7	8	9	10	11
Time interval 0	0	0	1	0	0	0	1	0	0	0

Ad hoc approach

1. Combining Open and Closed Models

    Pollock's (1981, 1982) original work was *ad hoc* rather than being based on a single likelihood. The prescribed procedures were to first select a closed model to estimate abundance based on data from secondary periods; and then select an open model to estimate survival between the primary periods by combining data from secondary periods; and finally estimate recruitment using the abundance estimates and survival estimates via the equation:

$$\hat{B}_i = \hat{N}_{i+1} - \phi_i \left(N_i - n_i + R_i \right),$$

where

$\hat{B}_i$	Number of births during $i \Rightarrow i+1$	n_i	Animals removed at i
N_{t+1}	Population size at time $t+1$	ϕ_i	Survival rate during the period $i \Rightarrow i +1$
N_t	Population size at time t	R_i	Number released at i

In this approach, model selection is carried out independently for the single open model and each of the K closed-model data sets. Williams et al. (2002) recommend using a single model for all of the secondary periods for consistency in assumptions and biases.

It is important to note that 2 types of capture probabilities must be estimated:

p_{ij} - the probabilities associated with **capture during the secondary sampling period** in the primary sampling period i , given that the animal was in the population at K_i and

$p_i{}^*$ - the capture probabilities associated with **capture at least once during the primary period** i, given that the animal was in the population at K_i..

Similar to CJS models primary capture probabilities may describe temporal variation and or behavioral trap response. Likewise, closed model p_{ij} can incorporate models of temporal variability, behavioral response, and heterogeneity. Permanent trap response (different recapture probability after first secondary capture period) can only be incorporated by splitting the data set into 2 groups and fitting the single open model and ($2K$-1) closed models, one for marked and one for unmarked animals in each of the primary periods except the first when all individuals are unmarked. Kendall et al. (1995) describes 24 possible models based on all combinations of the primary and secondary capture probability models.

Assumptions underlying the *ad hoc* modeling approaches described by Kendall et al. (1995) include those associated with closed-population models for secondary periods:

a. population is closed to gains and losses during the period,

b. marks are not lost nor incorrectly recorded,

c. the capture model structure is correct, and

d. fate of individuals is independent;

e. as well as, the assumptions associated with open models for the primary periods:

f. probability of surviving each period is the same for all animals,

g. capture probabilities are the same for each individual in the population at that time, and

h. capture and survival probabilities of individuals are independent.

Robust Design allows estimation of several parameters that are not estimable under either CJS or closed-population models. These include $\phi_{K-1} p_K$, the unidentifiable parameters in CJS, N_1, and B_1. Thus, under Robust Design the parameters

$$\hat{N}_1...\hat{N}_K \quad \hat{p}_1...\hat{p}_K \quad \hat{\phi}_1...\hat{\phi}_K \quad \hat{B}_1...\hat{B}_K$$

are all estimable.

Virtually any of the models possible with closed populations and open populations are possible with Robust Design because the primary and secondary periods are treated as independent. Furthermore, the probability of temporary emigration, that is the probability that an animal was not present on the study area during a given primary period, can be estimated from the 2 types of capture probabilities. Age specific models, reverse time models, and multistate models can all be used with Robust Design and in some cases the use of Robust Design permits the estimation of parameters of particular biologic interest.

Finally, because the closed population models used in the secondary sampling periods can incorporate individual capture heterogeneity, Robust Design can be used to estimate survival in the presence of capture heterogeneity. This is not possible using CJS open population models.

Likelihood-based approach

This approach differs from the original *ad hoc* approach in that Kendall et al. (1995) described the combined likelihood of the data from both the primary and secondary periods as the products of the components **including the mathematical relationships between their capture probabilities**.

1. Models

   Any of the closed models for which MLE have been described can be used with this approach. Thus, some of the original models incorporating heterogeneous capture probabilities are not possible at present. However, the use of mixture models which incorporate random effects may soon remedy that situation (Norris and Pollock 1996, Pledger 2000), and MARK has recently been modified to incorporate the Huggin's models with covariates of capture probabilities in Robust Design.

   Example model M_t^t which denotes time variation in capture probabilities in both primary and secondary periods with only 2 samples from each secondary period can be written as:

$$P\left(\{x_{0i}^\omega\},\{x_{hi}^\omega\}\right)=\left[P_1\left(\{u_i\}\mid\{U_i\},\{p_i^*\}\right)\right]$$
$$\times\left[P_2\left(\{m_{hi}\}\mid\{R_i\},\{\phi_i\},\{p_i^*\}\right)\right]$$
$$\times\left[P_3\left(\{x_{0i}^\omega\},\{x_{hi}^\omega\}\mid\{u_i\},\{m_{hi}\},\{p_{ij}\}\right)\right]$$

where

u_i	number of unmarked caught on at least one secondary occasion within primary period i
U_i	population of unmarked available for capture at i
m_{hi}	number marked during h (prior to i) caught on at least one secondary occasion within primary period i. Thus, $u_i + m_{hi}$ the number caught at least once during i.
R_i	number of marked animals released at i
r_i	number from R_i ever recaptured
p_i^*	probability of capture at least once during the primary period i,

	given that the animal was in the population at Ki..
p_{ij}	probability of capture during the secondary sampling period j in the primary sampling period i , given that the animal was in the population at Ki
$\{x_{0i}^{\omega}\}$	number previously unmarked exhibiting capture history ω over the secondary occasions within primary period i,
$\{x_{hi}^{\omega}\}$	number marked during primary period h unmarked animals exhibiting capture history ω over the secondary occasions within primary period i

m_{ij} is the number of recaptures from R_i captured at j, and, and

P_1 and P_2 are actually the unconditional components of the open population model.

The first component being the capture of unmarked animals:

$$P_1\left(\{u_i\}\mid\{U_i\},\{p_i^*\}\right)=\prod_{i=1}^{K}\left[\frac{U_i}{u_i!(U_i-u_i)!}\left(p_i^*\right)^{u_i}\left(1-p_i^*\right)^{U_i-u_i}\right]$$

where U_i and u_i are the numbers of unmarked animals in the population and the number of unmarked animals captured at i. The second component is the conditional probability of the recaptures (m_{ij}):

$$P_2\left(\{m_{ij}\}\mid\{R_i\},\{\phi_i\},\{p_i^*\}\right)=\prod_{i=1}^{K-1}\frac{R_i!}{(m_{i,i+1})!(m_{i,i+1})!...(m_{i,K})!(R_i!-r_i)!}$$
$$\times\left(\varphi_i p_{i+1}^*\right)^{m_{i,i+1}}\left[\varphi_i\left(1-p_{i+1}^*\right)\varphi_{i+1}\left(1-p_{i+2}^*\right)\right]^{m_{i,i+1}}...$$
$$\times\left[\varphi_i\left(1-p_{i+1}^*\right)...\varphi_{K-1}p_K^*\right]^{m_{i,K}}\chi_i^{R_i-r\,i}$$

where χ is the probability of not being recaptured. The third component of the likelihood models the data across the secondary periods in all of the different primary periods. For our example using 2 secondary periods over three primary periods:

$$P_3\left(\{x_{0i}^{\omega}\},\{x_{hi}^{\omega}\}\mid\{u_i\},\{m_{hi}\},\{p_{ij}\}\right)=\left(\frac{u_1!}{x_{01}^{10}!x_{01}^{01}!x_{01}^{11}!}\right)\left(\frac{p_{11}(1-p_{12})}{p_1^*}\right)^{x_{01}^{10}}\left(\frac{(1-p_{11})p_{12}}{p_1^*}\right)^{x_{01}^{01}}\left(\frac{p_{11}p_{12}}{p_1^*}\right)^{x_{01}^{11}}$$
$$\times\prod_{i=2}^{K}\left(\frac{u_i!}{x_{0i}^{10}!x_{0i}^{01}!x_{0i}^{11}!}\right)\left(\frac{m_{1i}!}{x_{1i}^{10}!x_{1i}^{01}!x_{1i}^{11}!}\right)...\left(\frac{m_{i-1,i}!}{x_{i-1,i}^{10}!x_{i-1,i}^{01}!x_{i-1,i}^{11}!}\right)\quad.$$
$$\times\left(\frac{p_{i1}(1-p_{i2})}{p_i^*}\right)^{x_i^{10}}\left(\frac{(1-p_{i1})p_{i2}}{p_i^*}\right)^{x_i^{01}}\left(\frac{p_{i1}p_{i2}}{p_i^*}\right)^{x_i^{11}}$$

The primary advantage of this approach is that the capture probabilities for the primary and secondary periods are linked via the equation:

$$p_i^*=1-\prod_{j=1}^{h}\left(1-p_{ij}\right).$$

Thus the probability of capture at least once during the primary period is the probability of not going uncaptured during all of the secondary periods. This equation is the basis for the joint modeling of the data from both types of sampling periods.

Similar to the other approaches a variety models for both open and closed populations can be implemented by constraining (reducing) the number of estimated parameters, through the use of time-specific or individual covariates.

2. Model assumptions

The assumptions of this approach are identical to those for the ad hoc approach with the addition of the relationship between the 2 types of capture probabilities.

One situation where this assumption is violated is when temporary emigration occurs among the primary sampling periods, thus some individuals are not available for capture during some secondary periods.

3. Estimation

In program MARK – Data types: Robust Design and Robust Design (Huggins est.).

The latter includes the ability to model heterogeneity as a function of recapture covariates.

Abundance estimation is via the equation:

$$\hat{N}_i = \frac{n_i}{\hat{p}_i^*}$$

Thus the number of new recruits is also estimable as in the ad hoc approach via:

$$\hat{B}_i = \hat{N}_{i+1} - \phi_i \left(N_i - n_i + R_i \right).$$

4. Model Selection, Estimator Robustness, and Model Assumptions

Since these models are based on the likelihood model selection via AIC is possible as are LRTs. Although robust GOF tests are not easily constructed, Williams et al. (2002) suggest that approaches based on contingency tables and bootstrap are reasonable.

In the absence of likelihood-based Robust design models that incorporate heterogeneity (but see Pledger 2000 and Huggins models), when heterogeneity is present it is expected that survival estimates would be relatively unbiased, while capture probabilities would be positively biased, and estimates of population size would be negatively biased.

Special estimation problems

1. Temporary Emigration

As already mentioned temporary emigration is a violation of the assumed relationship between the two types of capture probabilities and results in biased parameter estimates.

Kendall and Nichols (1995) and Kendall et al. (1997) develop estimators and models for use when temporary emigration occurs. Examples of when temporary emigration may occur include when home ranges of some animals are not completely sampled, when migratory patterns lead some animals to avoid the use of sampled areas during some periods, and when some animals become inactive during some sampling periods. Another example occurs in age-specific models when animals first appear as breeding adults.

Kendal et al. (1997) examined bias under two types of temporary emigration. Random temporary emigration occurs when each individual has the same probability of becoming a

temporary emigrant. Under this scenario capture probabilities are negatively biased and abundance estimates show positive bias. "Markovian" temporary emigration occurs when the probability of temporary emigration at time i is affected by whether an individual was a temporary emigrant at i-1. In this situation, the direction and magnitude of bias is dependent upon the nature of the Markov process.

The concept is that of the "superpopulation," N_i^0, which is the number of animals associated with the sampling area. Contrast this with N_i, the number of animals present at time i. The method still requires the assumption that the population is essentially closed during the secondary sampling periods. To understand the models we need to introduce the following additional random variables and parameters:

M_i^0	number of animals marked before primary period i and in the super population for the duration of the study.
M_i	number marked animals in the area during the primary period i
B_i^0	number of animals entering the superpopulation between primary periods i and i+1 and remaining in the superpopulation for the duration of the study.
B_i	number of animals entering the area during the primary period i
p_i^0	probability of capture for a member of the superpopulation during primary period i
p_i^*	probability of capture during i given present on the study area
γ_i	probability of temporary emigration (i.e., a member of N_i^0, but not available for capture).

a. Robust design with random emigration

Thus the relationship between the superpopulation and the population available during the sampling period is:

$$E\left(N_i \mid N_i^0\right) = \left(1 - \gamma_i\right)N_i^0.$$

Likewise the relationship between capture probabilities for the superpopulation and the available population is:

$$p_i^0 = \left(1 - \gamma_i\right)p_i^*.$$

An interesting result of this relationship is that the probability (rate) of random emigration can be estimated ad hoc from:

$$\gamma_i = 1 - \frac{p_i^0}{p_i^*}.$$

where p_i^* is the probability of capture during the secondary sampling periods and p_i^0 is the capture probability during open periods. It should be noted that this model is only valid under models that do not include capture heterogeneity.

In the full likelihood random emigration model proposed by Kendall et al. (1997) component P_2 of the likelihood, which deals with estimation of recapture during the primary periods is affected.

$$P_2^e\left(\{m_{ij}\}\mid\{R_i\},\{\phi_i\},\{p_i^*\},\{\gamma_i\}\right)=\prod_{i=1}^{K-1}\frac{R_i!}{(m_{i,i+1})!(m_{i,i+1})!...(m_{i,K})!(R_i!-r_i)!}$$

$$\times\left(\varphi_i(1-\gamma_{i+1})p_{i+1}^*\right)^{m_{i,i+1}}\left[\varphi_i\left(1-(1-\gamma_{i+1})p_{i+1}^*\right)\varphi_{i+1}\left(1-(1-\gamma_{i+2})p_{i+2}^*\right)\right]^{m_{i,i+1}}...$$

$$\times\left[\varphi_i\left(1-(1-\gamma_{i+1})p_{i+1}^*\right)...\varphi_{K-1}(1-\gamma_K)p_K^*\right]^{m_{i,K}}\left(\chi_i^e\right)^{R_i-r_i}$$

where χ_i^e is the probability of being in the superpopulation at during i (for initial capture) and never seen again. This model can be thought of as $\phi p_t \gamma_t$.. It should be noted that simply by imposing $\gamma = 0$, this model becomes $\phi_t p_t$.

b. Robust design with Markovian emigration

In this model emigration is modeled as a first order Markov process, i.e., it depends upon the state of the individual during the prior time period. Kendall uses the following additional notation:

γ'_i	probability of temporary emigration in primary period i given temporary emigration at i-1.
γ''_i	probability of temporary emigration in primary period i given **NOT** a temporary emigration at i-1.

Thus if $\gamma'_i = \gamma''_i$ the random emigration model is obtained. See Williams et al. (2001) or Kendall et al. (1997) for details of the likelihood. These models require many constraints because they condition on probabilities pertaining to animals not observed in the previous period.

These models are particularly useful for animal that have low breeding propensity (i.e., they do not breed in some years). For example, sea turtles, marine mammals, many seaducks, and seabirds.

2. Multiple Ages and Recruitment Components

The concept of Robust Design can be extended to multiple age groups. This is of particular interest because the components of recruitment can be separated into *in situ* reproduction on the study area and immigration from outside the study area (see Nichols and Pollock 1990 and Yoccoz et al. 1993). If this is of interest, study design is critically important. The time between primary sampling periods should correspond to the time required for young to mature into adults (or the next stage of interest). For example, animals classified as young during i can be assumed to be adults at $i+1$, and any other new adults on the area are assumed to be immigrants.

This approach has been extended to multiple age classes and multiple patches (Nichols and Coffman 1999).

3. Catch-Effort Studies

Robust design has also been extended to removal studies that incorporate information on sampling effort (Gould and Pollock 1997). This approach requires an initial release of marked animals just prior to the first removal sampling. Survival for marked and unmarked animals is

assumed to be equal, and secondary-period removals are used to estimate capture probabilities within primary periods for both marked and unmarked animals. This method allows the estimation of unmarked and total animals as well as recruitment for each primary period, and through simulation has been show superior to methods based on regression.

4. Potential for Future Work

5. Study Design

    a. Number of secondary periods – trade off between precision and model complexity versus population closure.

    b. If closure is false, open models can be used, but heterogeneity can not be examined.

    c. Biological motivation for the study – temporary emigration rates may be of primary interest

        1) Breeding rates
        2) Recruitment – reproduction and immigration

    d. Benefits

        1) Robust Design minimizes covariation between estimated parameters thus producing more precise estimates of the parameters of interest.
        2) Parameters that are otherwise inestimable – the final survival rate in open models, and in closed models the first and last recapture probabilities and abundances.
        3) More precise estimates of demographic rates due to increased captures in primary periods.

Time symmetrical (reverse-time capture history) models

1. Motivation

    Pollock et al. (1974) first suggested that capture history data were symmetrical with respect to time. Models we have examined thus far estimate conditional probabilities of survival and recapture given that an individual was know to be alive at some earlier time. Time symmetrical or reverse-time models attempt to estimate the probabilities of membership and recapture in the population at earlier time periods given capture at some later time.

    Another way to think of this is that recruitment with no mortality (backward) is statistically equivalent to mortality with no recruitment (forward).

    Building upon this concept, Pradel (1996) developed a suite of model using reverse time capture histories to estimate the proportion of the population that was previously in the population. The simplest model estimates recruitment to the population and is referred to as the Pradel recruitment only model.

2. Data structure

    Live capture histories consisting of 1s and 0s – the same data that are required for CJS models.

    Conceptually possible to develop probability distribution and likelihood based on a "reverse m – array" of final captures at each occasion and captures at time j that were most recently captured at time i. But much easier to develop models from standard capture history data. So the m-array remains the same. We simply need to redefine cell probabilities for the reverse-time models.

3. Model Structure

a. New parameters

γ_i –   seniority probability, probability that an animal present just before time i was already present just after time i - 1. (i.e., the animal did not enter the population during the interval i -1 to i.) This animal is "old." Conversely, 1- γ_i is the probability than an animal was recruited to the sampled population since just after i -1.

p'_i –   recapture probability at time i given present at (just after) i.

ε_i –   probability of not being seen prior to i given present just before i (Analogous to χ_i, and the final term in the multinomial) Thus, this includes animals that did not survive from $i – 1$, or was in the population and not seen at or before $i – 1$.

b. Losses or removal on capture

It is impossible for animals removed or killed on capture at i -1 to be recaptured at i.; therefore, it's important to define the above parameters carefully with respect to the sampling period. In open models, we deal with this situation implicitly by not including those individuals in the number of new releases just after i.

	Releases at i	Encounters at time j			
i	R_i – new releases	2	3	4	5
1	R_1	m_{12}	m_{13}	m_{14}	m_{15}
2	$R_2+m_{12}+m_{13}+m_{14}+m_{15}$		m_{23}	m_{24}	m_{25}
3	$R_3+m_{23}+m_{24}+m_{25}$			m_{34}	m_{35}
4	$R_4++m_{34}+m_{35}$				m_{45}

Furthermore, it has been shown that the estimates of Φ are relatively robust to heterogeneity in recapture probabilities in forward-time modeling.

c. Capture history example

Capture history: 011010

Capture at periods 2,3,5 in a 6-year study. Remember: time symmetrical or reverse-time models attempt to estimate the probabilities of membership and recapture in the population at earlier time periods given capture at some later time.

$$P(011010 | \text{last capture at } i = 5) = \gamma_5 (1\text{-}p'_4)\ \gamma_4 p'_3 \gamma_3 p'_2 \varepsilon_2$$

Translation: Probability that, given capture at 5, this animal survived period 5, was not captured at 4, survived time 4, was captured at 3, survived time 3, was captured at 2, but was not seen before time 2.

d. Multinomial probability and likelihood

It should be obvious from the above that we can construct a multinomial probability distribution and likelihood. For example in a study with 3 encounter occasions we have:

$$P(x_\omega) | R'_3)P(x_\omega) | R'_2),$$

where the R'_i are the number of animals last seen at i. Decomposing the above yields:

$$P(x_\omega) \mid R'_3) = \frac{R'_3!}{\prod_{k=1}^{\omega} x_\omega!} (\gamma_3 p'_2 \gamma_2 p'_1)^{x_{111}} (\gamma_3 p'_2 \varepsilon_2)^{x_{011}} (\gamma_3 (1 - p'_2) \gamma_2 p'_1)^{x_{101}} \varepsilon_3^{x_{001}},$$

and

$$P(x_\omega) \mid R'_2) = \frac{R'_2!}{\prod_{k=1}^{\omega} x_\omega!} (\gamma_2 p'_1)^{x_{110}} \varepsilon_2^{x_{010}}.$$

Although the history 100 is possible, it does not contribute to the probability distribution because no encounters occur prior to period 1.

e.   Alternative parameterizations

Pradel (1996) also described 3 other parameterizations of the reverse-time model. First it must be understood that Pradel accomplished this by simultaneous modeling of rates associated with forward-time and reverse-time models. He first established the relationship between the capture probabilities of the 2 approaches. The difference between the recapture probabilities is incorporated in the equation:

$$p'_i = \frac{p_i}{1 - p_i(1 - \eta_i)},$$

where η_i is the rate of re-release after capture. Thus, when $\eta_i = 1$, $p'_i = p_i$. The simultaneous modeling conditions on the population size just prior to the first occasion ($N_1^- = B_0$) and then calculates the expect population size at later times based on the expected change in population size over time (λ_i). Thus, the expectation is that

$$\lambda_i = \frac{N_{i+1}^-}{N_i^+}$$

and that

$$N_i^+ \varphi_i \approx N_{i+1}^- \gamma_{i+1}$$

Thus it follows that

$$\lambda_i = \frac{N_{i+1}^-}{N_i^+}$$
$$= \frac{\varphi_i}{\gamma_{i+1}}$$
$$= \frac{\varphi_i [1 - p_i(1 - \eta_i)]}{\gamma_{i+1}}.$$

Thus, we can rewrite the expected number of individuals exhibiting the capture history above as:

$$\mathrm{E}(x_{011010} \mid N_1^-) = N_1^- \lambda_1' \varepsilon_2 p_2 \eta_2 \varphi_2 p_3 \eta_3 \varphi_3 (1 - p_4) \varphi_4 p_5 \eta_5 \chi_5$$

incorporating important aspects of both likelihoods. Translated, the term $N_1^- \lambda_1'$ is the population size just before $i = 2$. ε_2 is the probability of not being caught before period 2. The remainder is the probability of capture and re-release on occasion 2 $(p_2 \eta_2)$, surviving from period 2 -3 and capture and re-release at 3 $\varphi_2 p_3 \eta_3$, surviving period 3-4 without capture at period 4 $(\varphi_3(1 - p_4))$, survival from 4-5 with capture and re-release at 5 $(\varphi_4 p_5 \eta_5)$, and finally not being captured after time 5 (χ_5).

The development of the probability distribution requires substitution for the initial population size N_1^-, which is the expected number of animals exhibiting each capture history divided sum of the expected number of animals first seen on each occasion. Thus, the generalized likelihood becomes:

$$L(x_\omega \mid \theta) = \prod_h P(h)^{x_h} = \prod_h \left(\frac{E(x_h)}{E(M)} \right)^{x_h} ,$$

where M is the total number of animals caught in the study. By substituting the following relationships into the likelihood, Pradel was able to develop 2 additional parameterizations using reverse-time approaches:

1) Survival and fertility (recruitment):

$$\gamma_i = \frac{\varphi_{i\text{-}1}}{\varphi_{i\text{-}1} + f_{i\text{-}1}}$$

2) Survival and lambda:

$$\gamma_i = \frac{\varphi_{i\text{-}1}}{\lambda_{i\text{-}1}}$$

4. Assumptions

    The assumptions of the reverse time models are similar to CJS models except homogeneity is assumed with respect to seniority and capture. The various ways of dealing with heterogeneity still apply – stratification, age-modeling, use of covariates.

   Probability of seniority is the same for all animals in each period.

    Capture probabilities are the same for each individual in the population at that time.

    Capture and seniority probabilities of individuals are independent.

5. Estimation

    MLE can be obtained by simply reversing the order of the capture histories and running through software for forward-time analyses (e.g., Resightings only model in MARK). MARK includes 4 different parameterizations for reverse time model that will be discussed below.

    Parameters estimable for a single-aged, time-specific K-period study include γ_K, γ_{K-1}, ..., γ_3 and p'_{K-1}, p'_{K-2}, ..., p'_2. Similar to CJS models γ_2 and
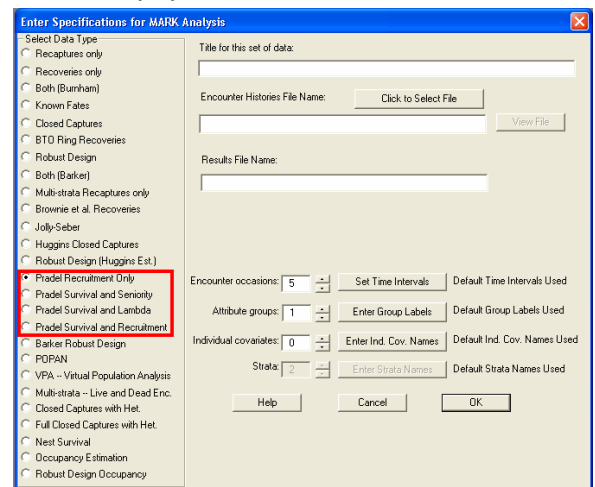
p'_1 can not be estimated separately, and in the case of no losses on capture the capture probabilities are identical to those obtained using the CJS model.

6.   Interpretation

(After Nichols et al. 2000) Consider an open population, where we define the growth rate, λ_i, as the realized change in population size of the time period i. Then it is reasonable to think of this parameter as:

$$\lambda_i = E\left(\frac{N_{i+1}}{N_i}\right).$$

We can also write the population size at $i+1$ as the number individuals surviving (remaining) since time i, L_i, plus the number recruited to the population since i, B_i. If we view L_i and B_i as binomial parameters given N_{i+1} and $B_i = N_{i+1} - L_i$ we can write the probability distribution of L_i as

$$P\left(L_i \mid N_{i+1}\right) = \frac{N_{i+1}}{(L_i)!(B_i)!}\lambda_{i+1}^{L_i}\left(1 - \gamma_{i+1}\right)^{(B_i)}$$

$$= \frac{N_{i+1}}{(L_i)!(N_{i+1} - L_i)!}\lambda_{i+1}^{L_i}\left(1 - \gamma_{i+1}\right)^{(N_{i+1}-L_i)}$$

Thus, γ_{i+1} can be viewed as the relative contributions to realized population growth. For example if $\gamma_{i+1} = 0.25$ (and $(1-\gamma_{i+1}) = 0.75$), then survivors have 3 times the impact on population growth in comparison to new recruits. These contributions can be shown analogous to the elasticities we will examine with matrix models.

7.   Alternative modeling

Reduced parameter models are of interest for parsimony and increasing precision of estimates. Use of multiple groups is also possible, as is the use of covariates of γ_i and p'_i. Models with capture history dependence (e.g., behavioral response) are not presently possible by reversing time in models.

8.   Model selection, estimator robustness, and model assumptions

Model selection via AIC is the same.

Goodness-of-fit tests based on contingency tables should be applicable, but have not been investigated in detail.

Estimator robustness should be viewed with caution. The robustness of the CJS survival estimator may not apply to the seniority estimator of the reverse-time model. For example trap response has little influence on CJS survival estimates because they are conditioned upon prior captures. Trap response should result in biased estimates of seniority from the time-symmetrical models. Trap-happy individuals result in over- estimates of capture probability and under-estimates of seniority and vice-versa. A similar situation exists when recapture probabilities of marked and unmarked individuals vary for other reasons.