

Robust Design Model

Changes in population size through time are a function of births, deaths, immigration, and emigration. Population biologists have devoted a disproportionate amount of time to models that assume immigration and emigration are non-existent. However, modern thinking suggests that these effects are quite important. For example, metapopulation dynamics are not possible without immigration and emigration in the subpopulations. In today's material, we will explore 2 models for marked animals that estimate emigration and immigration to a population, or group of populations. Although these models are complicated, they bring more biological reality to the analysis of population dynamics.

Pollock's Robust Design

The robust design model is a combination of the Cormack-Jolly-Seber (CJS) (Cormack 1964, Jolly 1965, Seber 1965) live recapture model and the closed capture models. The model is described in detail by Kendall et al. (1997, 1995) and Kendall and Nichols (1995). The key difference from the CJS model is that instead of just 1 capture occasion between survival intervals, multiple (>1) capture occasions are used. These occasions are close together in time, allowing the assumption that no mortality or emigration occurs during these short time intervals. The closely-spaced encounter occasions are termed "trapping sessions", and each trapping sessions can be viewed as a closed capture survey. The power of this model is derived from the fact that the probability that an animal is captured at least once in a trapping sessions can be estimated from just the data collected during the session using capture-recapture models developed for closed populations, such as those summarized by Otis et al. (1978). The longer intervals between trapping sessions allows estimation of survival, temporary emigration from the trapping area, and immigration of marked animals back to the trapping area.

Kendall et al. (1995, 1997) term the intervals between trapping sessions the *primary sampling periods*, where gains (birth and immigration) and losses (death and emigration) to the population can occur. *Secondary sampling periods* are the shorter intervals where the population is effectively closed to gains and losses.

For each trapping session (i), the probability of first capture (p_{ij}) and the probability of recapture (c_{ij}) are estimated (where j indexes the number of trapping occasions within the session), along with the number of animals in the population that are on the trapping area (N_i). For the intervals between trapping sessions, the probability of survival (S_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 $i - 1$ (γ''_i), and 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 $i - 1$ (γ'_i) are estimated. Indexing of these parameters follows the notation of Kendall et al. (1997). Thus, γ''_2 applies to the interval before the second primary trapping session, and γ'_2 is not estimated because there are no marked animals outside the study area at primary trapping session 2 that were also outside the study area at time 1 (because they could not have been marked otherwise).

To illustrate the model, assume a simple case with 3 trapping sessions, each consisting of 3 occasions. The encounter history is viewed as 9 live capture occasions, but with unequal spacing. Thus, the encounter history might be viewed as

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where \rightarrow separates the trapping sessions. The probability that an animal is captured at least once during a trapping session is defined as p^*_i , and is estimated as

$$p^*_i = 1 - (1 - p_{i1})(1 - p_{i2})(1 - p_{i3}).$$

That is, the probability of not seeing an animal on trapping occasion j is $(1 - p_{ij})$ for $j = 1, 2,$ and 3 . The probability of never seeing the animal during trapping session i is

$$(1 - p_{i1})(1 - p_{i2})(1 - p_{i3}),$$

so therefore, the probability of seeing the animal at least once during the trapping session is 1 minus this quantity. Note that the p_{ij} are estimated with the closed capture models.

To illustrate the meaning of the emigration (γ''_i -- probability that an animal is not available for capture, given that it was previously available for capture) and immigration (γ'_i -- probability that an animal is not available for capture, given that it was previously not available for capture) parameters, suppose the animal is captured during the first trapping session, not captured during the second trapping session, and then captured during the third trapping session. One of many encounter histories that would demonstrate this scenario would be (where a space indicates a primary interval):

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The probability of observing this encounter history can be broken down into 2 parts. First, consider the portion of the probability associated with the primary intervals. This would be

$$S_1 S_2 [\gamma''_2(1 - \gamma'_3) + (1 - \gamma''_2)(1 - p^*_2)(1 - \gamma''_3)] p^*_3.$$

The product in front of the first bracket ($S_1 S_2$) is the probability that the animal survived from the first trapping session to the third trapping session. Because we captured it alive on the third occasion, we know the animal survived both intervals. The complicated term in the brackets represents the probability that the animal was not captured during the second trapping session. The first product within the brackets [$\gamma''_2(1 - \gamma'_3)$] is the probability that the animal emigrated between the first 2 trapping sessions (γ''_2), and then immigrated back onto the study area during the interval between the second and third trapping sessions ($1 - \gamma'_3$). However, a second possibility exists for why the animal was not captured, i.e., that it remained on the study area and just was not captured. The term $(1 - \gamma''_2)$ represents “remained on the study area”. The term

$(1 - p^*_2)$ represents “not captured”. The final term $(1 - \gamma''_3)$ represents the probability that the animal remained on the study area so that it was available for capture during the third trapping session.

The second portion of the cell probability for the above encounter history involves the estimates of p^*_i , and is thus just the closed capture model probabilities.

To provide identifiability of the parameters for the Markovian emigration model (where an animal “remembers” that it is off the study area) when parameters are time-specific (i.e., t model), Kendall et al. (1997) suggest setting $\gamma''_{k-1} = \gamma''_k$ and $\gamma'_{k-1} = \gamma'_k$, where k is the number of trapping sessions. Otherwise, these pairs of parameters are confounded. To obtain the “No Emigration” model, set all the γ parameters to zero. If all the γ''_i are set to zero, then the γ'_i must all be set to zero also, because, there are no animals allowed to emigrate to provide a source of immigrants back into the population. To obtain the “Random Emigration” model (where the availability of the animal for capture is not a function of its status during the previous primary session), set $\gamma'_i = \gamma''_i$. This constraint is not intuitively obvious. The interpretation is that the probability of emigrating during an interval is the same as the probability of staying away. Biologically, the probability of being in the study area during the current trapping session is the same for those animals previously in and those animals previously out of the study area during the previous trapping session. The last survival parameter, S_{k-1} , is also not estimable under the t model unless these constraints are imposed. That is, the parameters γ''_{k-1} , γ''_k , γ'_{k-1} , γ'_k , and S_{k-1} are all confounded. Setting the constraints $\gamma''_{k-1} = \gamma''_k$ and $\gamma'_{k-1} = \gamma'_k$ makes the resulting 3 parameters estimable.

To specify the trapping sessions in Program MARK, the Time Interval lengths are used. The time intervals between the encounter occasions within a trapping session have a length of zero, whereas the time intervals between trapping sessions have a positive (>0) length. Mortality and emigration can only occur during these longer intervals. An example will make this clearer.

Assume that animals are trapped for 15 separate occasions over 5 years. The first year, animals are trapped for 2 days, the second year for 2 days, the third year for 4 days, the fourth year for 5 days, and the fifth year for 2 days. The number of encounter occasions would be specified as 15, because animals were trapped on 15 separate days. To indicate the intervals where mortality and emigration takes place, versus the short intervals within trapping sessions, the lengths of the time intervals would be specified as: 0,1,0,1,0,0,0,1,0,0,0,0,1,0. That is, only 14 time intervals are needed, where the value 1 means that 1 year elapsed. This mechanism is flexible, but can be a bit tricky. Note that all trapping sessions must have at least 2 occasions. Thus, you will never have 2 consecutive time intervals of length >0 .

Within each attribute group, a separate PIM is created for each of the parameters S_i , γ''_i , and γ'_i . A separate PIM is created for each trapping session for p_{ij} , c_{ij} , and N_i . Thus, a set of encounter histories with 5 trapping sessions would have 18 PIMs for each group.

Individual Covariates cannot be used with the Robust Design data type for the p_{ij} , c_{ij} , and N_i , but can be used with the Huggins (Huggins 1989, 1991; Alho 1990) robust design data type. However, the Huggins robust design data type does not estimate N as a parameter directly from the likelihood. Individual Covariates can be used to model the parameters S_i , γ''_i , and γ'_i in the Robust Design data type.

Literature Cited

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