

8. Mark-recapture analysis

Using MARK to estimate survival rates and population size with open population models

In this practical session, we use MARK to estimate annual survival rates for two populations of humpback whales. We also investigate the use of open population models to estimate population size for these data.

Remember that, without additional information, survival rates estimated from mark-recapture models are apparent survival rates because they also incorporate any permanent emigration.

We start with the West Greenland humpback whale dataset used in the previous practical sessions.

1. Entering data into MARK

First make a copy of the datafile **WGHumpback.inp** with name **WGHump_open.inp**, or something similar. This is so that you don't overwrite your previous results.

Open program MARK.

Select **File > New File** on the toolbar and select **Live recaptures CJS** from the list on the left. CJS is the commonly-used abbreviation for the Cormack-Jolly-Seber survival model.

Type in a title for the analysis, e.g.: 'WG humpback survival'.

For **Encounter Histories File Name**, select the file **WGHump_open.inp** input file.

Check the data using **View File**. Make sure you have **6 Encounter occasions**, ignore the part about **Attribute groups** and click **OK**.

2. Estimating annual survival rates

You should now see the PIM window called: **Apparent Survival Parameter (Phi), etc.** This window has a triangular matrix of small boxes representing the annual survival probabilities (columns) of cohorts of animals marked in a given year (rows). By default, they are set so that all animals seen in a given year have the same probability of survival to the next year, regardless of the cohort, giving five parameters. The model is thus set up to estimate survival from year 1 to 2 (parameter number 1), year 2 to 3 (parameter number 2), etc.

Now select the other PIM window: **Recapture Parameter (p), etc.**, which has an equivalent matrix of small boxes representing the annual recapture probabilities (columns) of cohorts of animals marked in a given year (rows). They are again set so that all animals seen in a given year have the same probability of recapture in a given year; five more parameters (no recaptures in the first year).

Close the two PIM windows and select **PIM > Parameter Index Chart** to check your current model.

Run your current model. Give the model a name such as "CJS $\phi(t)p(t)$ ". Remember, conventionally, **(t)** indicates that a model parameter varies over time.

Under **Link function**, choose **Logit**, as before.

Look at your results. There are five estimates of survival probability (**phi**) and five estimates of recapture probability (**p**). Record your results below.

Time-varying survival probability model

1:Phi = _____; SE = _____

2:Phi = _____; SE = _____

3:Phi = _____; SE = _____

4:Phi = _____; SE = _____

5:Phi = _____; SE = _____

6:p = _____; SE = _____

7:p = _____; SE = _____

8:p = _____; SE = _____

9:p = _____; SE = _____

10:p = _____; SE = _____

Note that the estimate for the final **Phi** parameter is effectively the same as the final **p** parameter and they have huge standard errors. This is because, in the full CJS model, these two parameters are confounded (cannot be estimated separately). We must therefore ignore the final estimate of survival probability. This is true for all models with time-varying survival.

The estimates of survival probability are quite variable and two of them have hit the maximum logical bound of 1.0 (or very nearly so). This is not very realistic and a next step could be to try a more parsimonious model with a single parameter for survival probability across all years.

Open the **Parameter Index Chart** (blue bars) again. Right click on the block of **phi** parameters (numbers 1 to 5) and select **Constant** to reduce the five time-varying survival probability parameters to a single parameter across all years. Close up the gap between the parameters.

Now run this model, giving it a suitable name, e.g. "CJS phi(.)p(t)". Remember, conventionally, (.) represents an unvarying (constant) model parameter.

In the **Results Browser**, compare the model diagnostics for this model with the previous model.

Note that this model **CJS phi(.)p(t)** has 6 parameters (1 for survival probability and 5 for recapture probability) as expected. However, the previous model **CJS phi(t)p(t)** only shows 7 or 8 parameters, even though it has 5 for survival probability and 5 for recapture probability. This is because MARK has not estimated (a) the final survival probability or (b) one or two of the survival probabilities that have hit the bound of 1.0.

To make a valid comparison of AICc, we must adjust the number of parameters in the **CJS phi(t)p(t)** model to 9 (not 10 because of the confounding of the final survival and recapture probability parameters).

Select **Adjustments > Number of parameters** from the toolbar. Increment the number of parameters to 9 and close the window. The diagnostics for this model have now been adjusted in the Results Browser, allowing a valid AICc comparison. The AICc has increased because of the increase in the number of parameters.

You need to do this for all models in which not all parameters have been estimated to make a valid comparison using AIC.

Question 1. Is the model with constant survival better than the model with time-varying survival?

Look at the results and record them below.

Constant survival probability model

1:Phi = _____; SE = _____

2:p = _____; SE = _____

3:p = _____; SE = _____

4:p = _____; SE = _____

5:p = _____; SE = _____

6:p = _____; SE = _____

Question 2. Does the estimate of survival rate seem reasonable for humpback whales? What annual mortality rate is equivalent to this estimate of annual survival?

All things considered, which would you choose as your best model and why?

3. Sex specific survival rates

The next exercise is to look for evidence of sex-specific survival in humpback whales using a different dataset. Go to **File > New File** on the toolbar in MARK to quit the previous analysis and start a new one with a different dataset. Remember, everything from your previous analysis is already saved.

Choose **Live Recaptures (CJS)** from **Select data type** again. Select the data file **GOM_hump_sexed.inp**. Look at the data. There are 14 sampling occasions (years) – enter this for **Encounter occasions**.

At the end of each row is either **1 0;** or **0 1;** indicating that animals have been assigned to one of two groups; the first group (**1 0;**) or the second group (**0 1;**). In these data, group 1 is Female and group 2 is Male. Enter **2** for **Attribute groups**. Use **Enter Group Labels** to label group 1 as **Female** and group 2 as **Male**. Click OK.

In this model there are four **Parameter Index Matrices**: apparent survival and recapture probabilities for females, and the same for males. Check the **Parameter Index Chart**; this model has a lot of parameters. Run the current model, giving it a suitable name.

Look at the results. There are 26 estimates of survival probability, 13 for females (1:Phi-13:Phi) and 13 for males (14:Phi - 26:Phi), and 26 estimates of recapture probability, 27:p-39:p for females and 40:p-52:p for males.

Question 3. How variable are the estimates of survival probability for this analysis? Is this a good model? Why (not)?

In this study/dataset, there is no reason why females and males should have different recapture probabilities, so try a model in which recapture probability is the same for females and males but still varies by year.

When you've run it, don't forget to check whether the number of estimated parameters for this model is the number that should be estimable (37 in this case because the final survival for both females and males are confounded with the final recapture probability). Adjust, if necessary, as before.

Also, don't forget to do this for the previous model, which has 50 estimable parameters.

Question 4. Is this model better? Is there still room for improvement?

Now try a model in which survival probabilities do not vary over time. Modify your current model so that it has a single survival parameter for females and a single survival parameter for males; that is, survival is constant over time but still varies by sex. Record these sex-specific estimates of survival probability.

Phi (females): _____; SE = _____

Phi (males): _____; SE = _____

Question 5. Is this model an improvement over previous models?

Finally, with this dataset, try a model with a single survival parameter for females and males combined; that is, survival varies neither by time nor by sex. Record your estimate of survival probability.

Phi (females & males): _____; SE = _____

Question 6. Is there evidence for a sex-specific difference in survival rate?

4. Open population estimation of population size

Open population models can also be used to estimate population size but they can be difficult to fit. Try this for Gulf of Maine humpback whales.

Go to **File > New File** to start a new analysis. Select the data file **GOM_hump_all.inp**, which is the same dataset as before (14 sampling occasions) but without the two groups for females and males.

Choose **Jolly-Seber** for the data type.

Look at the **Parameter Index Chart**. This model has 13 apparent survival (**Phi**) parameters, 14 capture/recapture (**p**) parameters, 13 **Lambda** parameters, and one initial population size (**N**) parameter. **Lambda** is a proportional measure of recruitment into the population; e.g. a value of 1.05 would mean a recruitment of 5% per year.

Close the **Parameter Index Chart** and run the model.

You may get an error saying that numerical convergence was never reached; i.e. the model fitting routine couldn't find a satisfactory maximum likelihood estimate. Or the model may run but the results are meaningless. A likely reason is that the model is over-parameterised (has too many parameters).

Try a reduced model with a single constant survival parameter and a single constant lambda parameter across all years.

Question 7. Do the results of this model seem reasonable?